Patterns in the space use of the Bearded Reedling, *Panurus biarmicus,* on the Tay Reedbeds, Scotland

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Summary

This thesis presents research into the space use of a specialist reedbed Passerine, the Bearded Reedling, or Bearded Tit, *Panurus biarmicus,* with a view to inform the conservation of this species and reedbeds as a whole. How a species uses space, and how space use changes between individuals or over time, can influence: the ability to forage and hunt effectively, breeding success, susceptibility to predation, genetic health, disease spread, robustness against environmental change and ultimately, colonisation or extinction. Thus, understanding the space use of animals can provide critical insight into ecological systems.

Birds offer interesting models when studying animal space use, as, by being intrinsically mobile, many bird species can occupy multiple spatial scales. As a consequence of being completely dependent on patchy and ephemeral reedbed habitats, the Bearded Reedling, has a clustered, inhomogeneous distribution throughout its range. This drives the existence of distinct spatial scales upon which space use studies should be characterised. Distribution and movement within a single reedbed can be considered local-scale, while spatial processes between reedbeds can be considered wide-scale. Temporal processes may act upon both of these scales. For example, changing interactions with predators may influence nest positioning at a local-scale, while seasonal changes in resource requirements might drive processes such as migration at a wide-scale.

The Bearded Reedling has a wide temperate breeding range, extending over much of Eurasia. On the IUCN's red list, it is listed as 'of least concern', with an estimated European population between 240,000-480,000 breeding pairs. Despite its relatively favourable conservation status, its dependence on reedbed habitats drives a fragmented distribution, with populations being concentrated in small, isolated, stands. Over the last century reedbed wetlands have suffered rapid declines caused by drainage schemes undertaken to improve land for development or agriculture. Additionally, many remaining reed stands are subject to extensive commercial management to produce thatch or biofuel. Conversely, in other areas, management is driven by conservation motives which recognise the present threats to reedbeds, and aim to encourage the diversity of species associated with these habitats. As the Bearded Reedling is fundamentally linked to the quality and structure of a reed stand, understanding the space use of this species will offer information for the direct conservation of this specialist species, and for the effects of reedbed management as a whole.

This thesis first presents studies of space use at a local-scale. All local-scale research is conducted at the Tay Reedbeds in eastern Scotland. Mist netting and bird ringing data are used

within capture recapture models, which include an explicit spatial component, to gain insight into the abundance of the Bearded Reedling on the Tay. This abundance estimation approach suggests the Tay reedbeds are a stronghold for this species on the British Isles, and that, as a high latitude site, the Tay may have importance for range expansion. A combination of transect surveys and radio-tracking data are then used to establish the local-scale space use of this species during the breeding and autumnal seasons. These data are related to changes in the structure of reed caused by local management in the form of mosaic winter reed cutting. Results suggest that birds exploit young and cut patches of reed as foraging resources when they are available, and that old, unmanaged reed is critical for nesting and winter foraging.

Further local-scale studies concern the spatial patterns in the nesting habits of this species. Mosaic reed cutting creates clear edges in a reedbed. Artificial nests placed in the Tay Reedbeds demonstrate increased nest predation rates closer to the edges of cut patches. Additionally, high predation rates become reduced as the cut reed re-grows, suggesting that reed cutting may increase accessibility of the stand to predators. As Bearded Reedling nests are uncommon and difficult to locate, the timing, site selection and structure of a sample of real nests from the Tay is then detailed. These demonstrate an early, and relatively rigid breeding onset in this species, the importance of dense, compacted reeds as nesting sites and a degree of flexibility in nest structure.

Conservation efforts will also benefit from studies into wide-scale spatial processes. These may be important when establishing how colonisation events occur and when predicting the effects of climatic change. The Bearded Reedling has been traditionally considered a resident species which only occasionally undertakes wide-scale, between-reedbed, movements. Indeed, the ecology of this species suggests strict year round local residency to reedbeds, with distinct seasonal changes in diet allowing occupation of these habitats year round. The European ringing recoveries of this species, since the 1970s are investigated to better characterise the wider movements of specialist resident. These suggest residency in southern populations, but higher instances of movement than expected in more northerly regions. In these regions wide-scale movement patterns resemble those of partial regular migratory species.

An understanding of local and wide-scale spatial processes can offer a strong foundation on which to build conservation strategies. This thesis aims to use studies of space use to provide this foundation for the Bearded Reedling and offer further insight into the ecology of reedbed habitats as a whole. The thesis concludes by proposing an effective strategy for the conservation management of reedbeds that will especially benefit the Bearded Reedling.

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Author Declaration

I declare that the work presented in this thesis is my own unless otherwise stated, and that no part of this thesis has been submitted for any other degree. The following lists the various contributions made to the material in this thesis by co-authors and collaborators:

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Chapter One

General Introduction

Biodiversity is under severe threat from human influence. Species are faced with a rapidly changing climate (Thomas *et al.* 2004) and continual modification or destruction of their environments (Fischer and Lindenmayer 2007). Extinction is imminent for many species (Ricketts *et al.* 2005), and for many others, direct measures must be undertaken within the next decades in order to provide, at least, the possibility of their survival (Possingham 2000, Wilson 2003). These measures may come in the form of conservation, which seeks to increase the distribution and abundance of species or habitats in order to minimise their risk of extinction. Conservationists are, thus, tasked with ensuring the significant social, health and economic benefits provided by a rich and biodiverse environment are afforded to future generations.

While the decline of biodiversity is most apparent in the tropics (Turner 1996), it remains conspicuous in temperate latitudes. Here, gradual climatic change may alter seasonal profiles, having implications for the synchrony between the yearly cycles of many plants and animals (Root *et al.* 2003, Stevenson *et al.* 2015). Additionally, the modification of vast landscapes undoubtedly reduces the space for biodiversity, commonly simplifying habitats into urban or agricultural areas (Fischer and Lindenmayer 2007). The remaining patches of even semi-natural habitats have become increasingly fragmented and isolated, limiting populations to few protected refuges (Fahrig 2003). Additionally, for some species, the ubiquitous backdrop of a changing climate and dramatic habitat modification, has been combined with persistent persecution and over-exploitation (Magnin 1991, Whitfield *et al.* 2004), to further increase pressures. As a consequence, 17% of plant and animal species in Europe, assessed by the IUCN, are threatened with extinction (IUCN 2015).

Clearly, the high proportion of threatened species makes it impossible to fund and implement directed conservation for each. Thus, realistic strategies include prioritising species which indicate the overall status of a given habitat (Noss 1990), or those that can act as a flagship to raise awareness for conservation issues (Branton and Richardson 2011). Bird species are a group which can often fulfil these requirements. Birds are highly dependent on climatic conditions, having strict seasonal phases such as breeding, migration and moult, which must occur in close synchrony to changes in the wider environment (Both and Visser 2005, Visser *et al.* 2010). Additionally, the often conspicuous presence, or absence, of bird species from an area can offer a clear indication to

the quality of a local habitat (Noss 1990). Finally, bird species are engaging and emotive, with their wide diversity of form combined with stories of migration or breeding, being able to capture public interest and raise the support necessary to implement protection. Indeed, many bird species are of conservation concern themselves, with 13% of European species threatened, and 2% critically endangered (BirdLife International 2015). 25% of the 515 bird species which occur in Europe have undergone significant reductions since the 1970s (Balmer *et al.* 2013, BirdLife International 2015). Actions to conserve bird species, and the habitats they depend on, are, thus, a strong starting point when seeking to mitigate or reverse the loss of biodiversity.

Within birds, species that are highly specialised to a single, specific habitat may be some of the most vulnerable to environmental change and therefore in need of attention (McKinney 1997, Colles *et al.* 2009, Clavel *et al.* 2011). In many cases, specialist species have complex relationships with a particular habitat and slight changes to the environment, driven by either climate or local habitat modification, may have a considerable impact on the population as a whole. For example, Snow Buntings, *Plectrophenax nivalis*, are songbirds specialised to breeding in cold latitudes and may be outcompeted as a warming climate opens up these breeding grounds to more general species (Fossøy *et al.* 2014). Similarly, the modification of prey availability by changing fishing practices has driven sharp declines in several specialist seabird species (Monaghan 1992, Becker and Beissinger 2006). The delicate interactions of specialist species with their environments makes it unsurprising that they are more prone to extinction than generalists (Clavel *et al.* 2011), and it is, thus, of critical importance that such specialists are prioritised during targeted conservation.

A strong strategy for the conservation of specialist species is through the preservation and enhancement of their chosen habitat at key sites. Thus, an understanding of the complex relationships between specialist species and their environments is pivotal when implementing effective conservation. When certain factors are overlooked, even the most well-intended conservation management may do little to impede the decline of biodiversity, and, in some cases may even exacerbate losses further. A contemporary example involves the decline of farmland birds throughout Europe, caused by the move from traditional to intensive agriculture. In many countries government funded agri-environment schemes, which encouraged farming practices beneficial to farmland specialists, were implemented to promote recovery (Kleijn *et al.* 2006). However, there has been little evidence that species such as the Skylark, *Alauda arvensi*, or Yellowhammer, *Emberiza citronella,* are recovering in response to these schemes (Hammers *et al.* 2015). Further research is needed to establish the reasons for this, however winter congregation around measures such as fields sown with wild bird seed mixes may lead to continued declines by increasing disease spread

and predation (Kleijn *et al.* 2001, Kleijn and Sutherland 2003, Hammers *et al.* 2015, Żmihorski *et al.* 2016). All conservation projects, including those concerning the protection of specialist species and their habitats, should therefore, be based on a solid scientific foundation (Pullin and Knight 2003, Sutherland *et al.* 2004).

Such a foundation may be constructed from studies of animal space use. Observing spatial patterns in the distribution and movement of animals, and how these change throughout the environment and over time can offer valuable information for conservation. Spatial interactions between animals and their habitats can occur across a range of scales which combine to produce an overall pattern of space use. Understanding these patterns at local-scale, by observing daily, individual level distribution or movement, can offer insight into resource gathering (Manly *et al.* 2002), competitive interactions (Stamps 1991, Andrews *et al.* 2015) and predation (Hebblewhite *et al.* 2005). Conservation can directly benefit from this insight when identifying important features of the habitat to preserve for a given species, or establishing the importance of ecological factors such as predation in driving spatial heterogeneity. For example Tolon *et al.* (2009) show that the utilisation of a designated wildlife reserve by individual wild boar, *Sus scrofa,* was influenced by the risk of hunting pressures. On a wide-scale, where distribution is explored over vast regions, conservation can benefit from an understanding of how a species may colonise new areas (Greenwood 1980) or cope with a dynamic climate (Terrill and Able 1988, Newton 2010). Indeed, studies of multiple species at a wide-scale have been used to identify and advocate the protection of critical marine biodiversity hotspots (Lascelles *et al.* 2016).

The value of research into animal space use has led to the development of many practical techniques: distribution data can be collected directly using transect methods (Buckland *et al.* 2001), local-scale movements can be revealed with radio-telemetry (White and Garrott 1990), and wider movements with classic bird ringing techniques (Newton 2014) or, more recently, satellite telemetry (Kays *et al.* 2015). Further, for each of these methodologies, modern analytical techniques can be implemented to model spatial processes and provide conclusions which can be directly translated into conservation management (Manly 1977, Buckland *et al.* 2001, Beyer *et al.* 2010, Efford and Fewster 2013).

This thesis seeks to encompass an understanding of space use into the practical conservation of a highly specialist bird species. It aims to study the distribution and movement of this species, observing changes in spatial patterns at multiple scales, through use of spatial data gathering and analytical methods. These methods can be used to better establish the relationship of

this specialist species, with its specialist environment and provide a strong foundation upon which appropriate conservation measures can be implemented. These measures may include effectively managing habitat for this species, and gaining insight into how it might react to a changing climate. Thus, overall, this thesis aims to use an understanding of space use to assist conservation in achieving its ultimate purpose: to increase the distribution and abundance of an organism, and reduce its chances of extinction.

The Bearded Reedling, *Panurus biarmicus,* is a highly specialist, resident, reedbed Passerine. It is completely dependent on temperate reedbed habitats, having adapted to solely exploit these sites when nesting, foraging and wintering (Cramp and Perrins 1993). The affinity between this species and reedbed habitats is close enough that individuals can remain in a single reed stand their entire life. The species is not of direct conservation concern, being listed as 'of least concern' upon the IUCN's red list (BirdLife International 2014) due to its extensive range across Eurasia. However, the confinement of this species to reed means it is generally unseen, offering conservationists a distinctive and charismatic species with which to highlight due concern for the status of reed habitat as a whole. More importantly its specialisation and dependence on reedbed habitats, namely those consisting of continuous Common Reed, *Phragmites australis,* stands, mean it is intrinsically linked to the status of this specialist habitat. Measures of the presence and success of Bearded Reedling populations, therefore, act as strong indicators to the quality of given reed stands (Bibby 1983, Hoi and Hoi 2001), and the overall state of reedbed habitat in the wider environment.

In Europe, over the last century reedbeds have been in sharp decline due to wide-scale drainage schemes which have both dried out many established sites, and reduced the number of sites available for new reed to colonise (Hartog *et al.* 1989, Brix 1999). Further, this habitat is intrinsically temporal, being an intermediate stage of succession. After several years of growth, a diverse seedbank can build up in the accumulating leaf litter, eventually causing the stand succeed into scrubland (Hawke and Jose 1996). In many reedbeds throughout Europe, declines have been further exacerbated by the sudden appearance of the reed dieback phenomenon, where large areas of reed are retreating due to a combination of disturbance and eutrophication (Ostendorp 1989, Brix 1999). At a wide-scale, reedbed habitats are therefore isolated and fragmented, consequentially constraining the species dependent on these sites to distinct stands of varying size and detachment. Thus, with so few new sites becoming available, and the apparent threats to currently established reedbeds, conservation efforts must be placed into the protection and enhancement of key fragments of reedbed in order to protect this habitat and its dependent species.

This thesis therefore aims not only to protect a single species, but also to further our understanding of the interactions between reedbed specialists, their habitat, and the impacts of human influence on these interactions. Many reedbeds are subject to extensive anthropogenic management, for either commercial or conservation motives. Reed offers a valuable resource, from which an industry has been built around commercial harvesting for thatch or biofuel (Poulin and Lefebvre 2002, Kronbergs and Smits 2009). At its largest, this industry involves the mechanical cutting of previous year's growth during the winter, leaving patches of reed clear until rapid regowth during the spring. Alternative, conservation driven motives, could involve securing the long term integrity of the reedbed by preventing leaf litter accumulation (Cowie *et al.* 1992, Hawke and Jose 1996). This might be conducted by controlling water levels or consistent winter reed cutting at a smaller scale than commercial harvesting. These methods are used to stimulate the growth of reed stems and refresh the seedbank, impeding succession. Reed cutting for conservation may also be undertaken in order to create heterogeneity throughout the reedbed, producing a stand consisting of differently aged reed thought to offer breeding birds a mosaic of resources (Hawke and Jose 1996). Clearly, human actions, regardless of their motive, can have significant effects on the structure and lifecycle of a reedbed (Valkama *et al.* 2008) which are likely to have resounding impacts for the species dependent on reedbeds. For the appropriate conservation of reedbed communities, these impacts must be understood.

The thesis begins by synthesising the current literature concerning its central study organism, the Bearded Reedling (Chapter 2). It then aims to utilise an understanding of space use at, initially, a local-scale and subsequently a wide-scale, to answer questions relevant for the future conservation of this species. The confinement of the Bearded Reedling to isolated reedbed habitats allows the intuitive division of these scales of space use: local-scale space use may represent distribution and movement within a single reed stand, while space use at a wide-scale is defined as distribution or movements occurring between distinct reedbed fragments. The first research chapters (3 to 6) focus on questions relevant to the local-scale conservation of the Bearded Reedling, while the remaining research chapters (7 and 8) concern wide-scale problems.

All local-scale studies were conducted at a stronghold for this species at the Tay Reedbeds in eastern Scotland. The Tay Reedbeds are the largest continuous stands of *Phragmites* reed in the British Isles, totalling an area 4.1km^2 along the northern bank of the inner Tay Estuary. This site offers a useful system in which to study the local-scale conservation of the Bearded Reedling, being

managed in the form of winter reed cutting by conservation organisations in order to preserve the long term integrity of the reed, and create heterogeneity for the benefit of breeding birds. This site is also on the northern fringe of the species' range and may offer insight into the effects of wide climatic variation for this species.

Chapter 3 seeks to establish the numbers of Bearded Reedlings within this local site. It utilises a capture-recapture dataset compiled during a high effort mist-netting and ringing protocol undertaken at the Tay Reedbeds. While well established, traditional analytical methods for the estimation of abundance from capture-recapture data overlook the inherent spatial information contained within animal trapping data. This chapter seeks to demonstrate the use of a new suite of spatial capture-recapture models when estimating the abundance of the Bearded Reedlings on the Tay. These methods allow estimates, free of spatial bias, over a well-defined sampling region.

Having established the importance of this site from the perspective of abundance, Chapter 4 aims to provide reedbed management with quantifiable evidence concerning the consequences of reed cutting for the Bearded Reedling. This chapter directly measures local-scale space use to infer the resource selection processes of this species, and how these relate to reedbed management in the form of winter reed cutting. Measures of distribution at the population level offer insight into how the general population at the Tay reacts to management during different seasonal phases, while a selection of radio-tracked individuals demonstrate how this species interacts with management at a fine-scale.

Chapter 5 further investigates the effects of reedbed management, focusing directly on nest predation. An artificial nest experiment is used to establish whether an edge effect, where nests are predated more heavily close to the boundaries of habitats, is present at the edges of cut reed patches. Importantly, while contributing to the debate surrounding appropriate ways to manage reedbed habitat, this chapter also seeks to emphasise the importance of dynamic spatial and temporal processes in nest predation, which may have implications for habitat use. In this chapter, predation rates were investigated using artificial nests in order to prevent unnecessary disturbance to this protected UK breeding population. Despite this, in order to corroborate the artificial nest design and structure, a small number real Bearded Reedling nests were visited during the study, offering the first sample of these nests found in Scotland. As natural nests of this species are rare, especially from northern populations such as the Tay, Chapter 6 uses this sample of nests to perform

a detailed investigation into the timing, site selection and structure of natural Bearded Reedling nests.

Chapter 7 is the first of two chapters concerning the wide-scale conservation of this species. This chapter presents the results of a symposium concerning the conservation of Bearded Reedling across the UK which was organised and led as part of the current thesis project. The symposium was attended by delegates who have studied the Bearded Reedling at an array of reedbed sites subject to varying monitoring and management. The current threats to this species, monitoring methods and most appropriate means by which to manage reedbeds are highlighted and discussed, facilitating a move towards standardisation and more adequate national monitoring. The chapter thus extends and compares the findings from the Tay to those from across the United Kingdom, and applies the local research to nation-wide conservation efforts.

Chapter 8 concludes the research chapters with an investigation into the wide-scale seasonal movements of the Bearded Reedling. This species is strongly adapted to remaining within temperate reedbeds for the full year, with seasonal changes in gut morphology allowing it to change from a summer diet of invertebrates, to a winter diet of reed seeds. For the Bearded Reedling, as well as for other species strongly adapted to remaining as residents, the occasional wide-scale movements they undertake are poorly understood. This chapter utilises ringing recoveries of the Bearded Reedling throughout Europe to investigate the tendency of this species to undertake wide movements, and establish whether these movements show discernible dispersive or migratory regularities on a European scale.

The final chapter aims to synthesise the main findings of this thesis. Given the dynamic spatial and temporal processes discovered for the Bearded Reedling, these findings are built into an overall seasonal picture of its lifecycle, which draws upon both local-scale spatial processes, and those occurring at a wider-scale. This chapter aims to demonstrate how studies of space use conducted over multiple spatio-temporal scales, can enhance conservation strategies and offer guidance for the practical management of even the most highly specialised species.

Chapter Two

A review of the literature concerning the Bearded Reedling

Iain Malzer

2.1 Introduction

The Bearded Reedling, *Panurus biarmicus*, is a reedbed dwelling passerine. This species is only rarely encountered outside reedbeds, with such appearances being inconsistent and brief. Further, this species is distinct from other reedbed specialist passerines, such as many of the *Acrocephalus* warblers, in that it does not undertake a long distance migration, but it remains in temperate reedbeds for the full year. This strong year round affinity has led to the development of morphological and behavioural adaptations that allow this species to successfully inhabit reedbeds throughout every seasonal phase. Further, the distinctive, highly specialist, ecology of this species offers a unique perspective when studying population processes and systems of space use. As such, since 1970, the Bearded Reedling has been the main focus of 61 peer reviewed research papers available on the electronic database, Web of Science (*keywords: "Bearded Tit", "Bearded Reedling", "Panurus biarmicus"; Search conducted 21/09/2015*). This literature analysis focuses mainly on English language publications. However, there is a large body of observational information available on this species from continental Europe published in various languages, mainly: German, Czech and Dutch. While it is not currently within the scope of this review to evaluate all these observational papers, Wawrzyniak and Sohns (1986) and Elzen (1993) provide comprehensive summaries of this work, and are referenced throughout. Overall, this review aims to synthesise the current scientific literature concerning the Bearded Reedling, with the aim to demonstrate the uniqueness of this species, its current conservation status and identify areas that would benefit from further research.

2.2 Reedbed Habitats

As the Bearded Reedling is strongly associated with reedbed habitats, many of the questions surrounding the current conservation of this species may be answered with an understanding of the key processes driving the extent and occurrence of reedbeds. These habitats are found where terrestrial environments are frequently water-logged or flooded. They are an intermediate stage of natural vegetative succession in semi-aquatic areas. Depending on water levels, salinity, nutrient availability and climatic conditions fast-growing, water-tolerant pioneer species, especially grasses, sedges or rushes can spread quickly throughout areas of shallow water forming single species stands (Hawke and Jose 1996). These stands are often highly productive, with both rapid vertical and

horizontal growth occurring during the growing season. Eventually, as deep litter layers are built up, productivity is reduced allowing scrub species to colonise drier areas (Van der Troon and Hemminga 1994). While the persistence and structure of reedbeds may show extensive variation both temporally and spatially, stands can persist indefinitely when the accumulating litter layer is periodically washed away by flooding, grazing or cutting, impeding the later stages of succession (Hawke and Jose 1996, Beemster *et al.* 2010).

In Europe, Common Reed, *Phragmites australis,* is the dominant reedbed species. It can solely occupy vast stretches of marshland with areas such as Lake Valence in Hungary extending over 10km^2 (Báldi and Kisbenedek 1999). Such areas show a characteristic reedbed structure with dense, non-branching stems standing 2-5 metres high. This perennial grass blooms from July to November, producing purple panicles covered in spikelets. Each stem can produce thousands of seeds giving it a feathered appearance. Transferred by water and wind these seeds make up the greatest proportion of the reedbed's seed bank. They are, however, not the main means of reproduction in this species. More commonly rhizome nodes are broken off and carried by water currents, facilitating the rapid expansion of the stand. The reeds die back every winter, but the long woody stems persist, often still holding onto their seeds well into the winter. After the last frost, rapid re-growth will occur, with the next layer of new, green, stems reaching their full height by midsummer (Stance 2010).

Due to excessive water extraction and drainage, productive wetland habitats, including reedbeds, are in decline worldwide (Bibby and Lunn 1982). 40% of the UK's reedbed habitats were lost between 1940 – 1990 (Edom 2006). Additionally, in southern Europe, reed die-back, caused by the eutrophication and persistent disturbance of reed habitats has exacerbated declines (Brix 1999, Gigante *et al.* 2014). However, despite this overall decline *P. australis* is still present over a wide geographic range (Clevering and Lissner 1999), showing an array of different life strategies dependent on local environmental conditions. It occurs in freshwater systems of differing depths (Coops *et al.* 1996) and brackish or marine systems (Burdick *et al.* 2001) on every continent except Antarctica. Vretare *et al.* (2001) demonstrate this versatility and the potential for phenotypic plasticity within reed. When comparing samples grown in deep water to those grown in shallow water they noted fewer but taller stems. Larger stems in deep water allowed continued gas exchange and access to light. Similarly, Lessmann *et al.* (2001) show the variation in photosynthetic strategies when comparing samples from geographically distinct populations throughout Europe. Extensive variation in ploidy levels between genotypes has also been linked to the wide range of morphologies and ecotypes seen within this species (Clevering and Lissner 1999, Hansen *et al.* 2007).

Such genetic diversity and the plasticity within a given genotype have allowed this species to occupy a range of wetland environments.

This resilience over a wide range of environmental conditions has also offered uses for environmental health. In the Netherlands in 1967, Common Reed was used in the first free water surface constructed wetland, for the treatment of wastewater (Vymazal 2008). Its hardiness and ability to cope with changing water and nutrient levels have since seen this species used in a number of different reedbed water purification systems. Both aerobic and anaerobic processes occur around the rhizomes allowing the complete breakdown of toxic organic substances into less harmful inorganic substances (Vymazal, 2008). Several designs based on this technique, detailed in Vymazal's (2008) review, have been implemented worldwide for the treatment of many different wastewaters.

Common Reed has further anthropogenic value, being the most commonly used thatching material in Europe (Poulin and Lefebvre 2002). Within the last decade the UK had 60,000 homes with thatched roofs (Edom 2006). Although practices vary widely with the ecology and underlying geology of the area, reed cutting for thatch normally begins in January, when stems are dead and ceases in March, before new growth begins (Hawke and Jose 1996, Edom 2006). Young patches of reed, with only one or two years of growth are the easiest to cut, and tend to have straight stems, making the most effective thatch. Thus, 'single wale' reed cutting where the same patches of reed are cut every winter is the most commonly used commercial method. Rolling and burning of reed are occasionally implemented in dense old stands to initially clear the reed before single wale cutting is initiated on subsequent years. Similarly, where hydrological control is available, stands can be flooded during the growing season to ensure reed remains dominant. More recently, Sathitsuksanoh *et al.* (2009) suggest that Common Reed may have a further role as a biofuel, achieving high glucose yields upon burning.

Clearly, reedbeds have their own intrinsic conservation value and potential anthropogenic uses that should justify their conservation. However, added support for the conservation of these areas comes from the wealth of species reliant on them. These include plants such as the Crested Buckler Fern, *Dryopteris cristata,* Greater Water Parsnip, *Sium latifolium,* and Greater Spearwort, *Ranunculus lingua* (Cowie et al, 1992). Around 700 invertebrates are associated with reedbeds in the UK, of which 40 insect species are fully dependent on these habitats (Hawke and Jose, 1996). Reedbeds are also important sites for many endemic Lepidoptera species, including the Fenn's Wainscot moth, *Protarchanara brevilinea*, the larvae of which feed within the reed stems (Hawke and Jose, 1996). Of mammal species, Water Voles, *Arvicola amphibius* and Otters *Lutra lutra* may

exploit reedbeds extensive ditches and channels. Finally, these sites are critical for many specialist bird species such as Bitterns, *Botaurus stellaris,* Water Rail, *Rallus aquaticus*, Spotted Crake, *Porzana porzana*, Reed Warblers, *Acrocephalus scirpaceus* and Bearded Reedlings.

2.3 What is a Bearded Reedling?

The Bearded Reedling has a wide distribution stretching the extent of Eurasia (BirdLife International 2014, *See Figure 2.1*). Europe makes up around 50% of the global species range and has an estimate of 240,000–480,000 breeding pairs, Chinese and other Asian populations need further census (BirdLife International 2014). Due to its confinement to reedbeds, populations of Bearded Reedlings are highly fragmented and vary in size depending on the availability of the habitat. Populations of up to 50,000 individuals can occupy extensive reedbeds, on Lake Neusiedl in Austria (Hoi, personal communications). However, more commonly smaller reedbed fragments hold around 50 pairs, such as the 130 hectare reedbed, Leighton Moss, in northern England (Wilson 1993). The existence of three races over this extensive range has been suggested by Sluys (1982), *biarmicus* in west and north Germany, Europe, Iberia, Italy and part of Greece, *russicus* in eastern Europe, south Russia and towards the Caspian Sea, and *kosswigi* which is local to southern Turkey but now considered extinct (Svensson 1992, Saygılı *et al.* 2013).

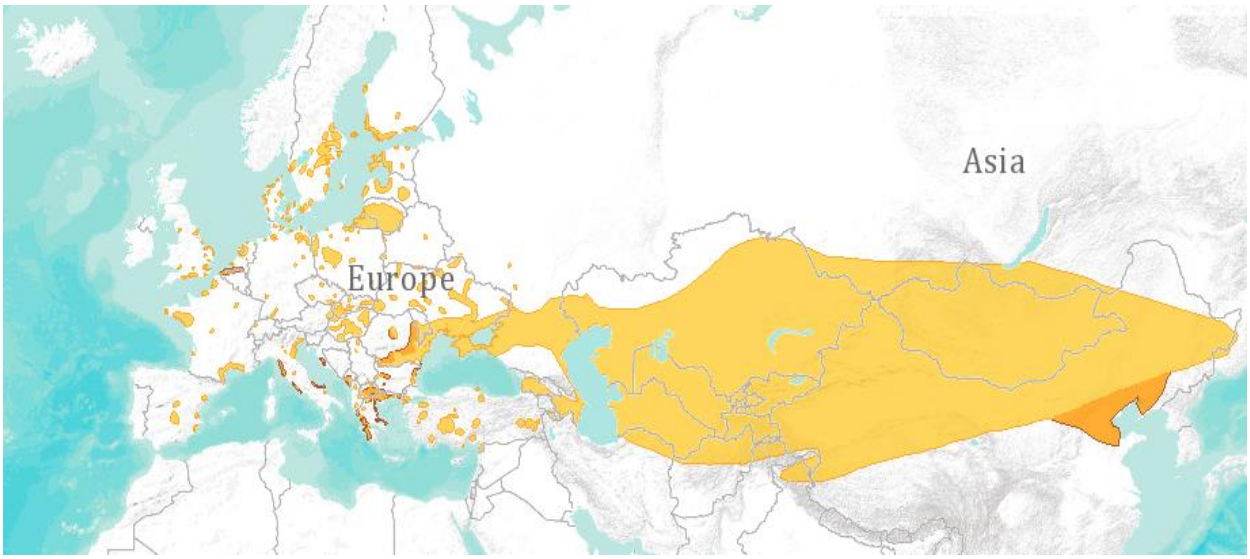


Figure 2.1 – Distribution of the Bearded Reedling according to the IUCN (BirdLife International 2014). *Dark orange areas have highest abundance. Asian populations lack detail due to limited census and monitoring.*

The position of this species within the Sylviidea passerines is ambiguous. Based on behaviour and morphology, early taxonomists placed the Bearded Reedling with the parrotbills (Diegnan 1964). However, the positioning of this species within the babblers was consistently disputed (Johansson *et al.* 2008). In more recent molecular studies *Panurus* was deemed monophyletic (Alström *et al.* 2006, Johansson *et al.* 2008). However, despite this, the position of this branch within the Sylviidea passerines remained unclear (Johansson *et al.* 2008). Jonsson and Fjeldsa (2006) demonstrate the enigmatic nature of this genus when trying to place it into an Oscine supertree. Similarly, when constructing phylogenetic histories using gene sequences Alström *et al.* (2006) reported conflicting trees from nuclear and mitochondrial DNA. Cyctochrome B trees placed *Panurus* as a sister group to the *Sitta* (treecreepers) while phylogenies derived from myoglobin suggested the Bearded Reedling was sister to the *Alaudidae* (larks). Fuchs *et al.* (2006) supported the latter relationship. Fregin *et al.* (2012) provide the most recent and comprehensive genetic investigation into the relationships between members of this superfamily, using one mtDNA and six nuclear markers, to find support for the *Panurus* - *Alaudidae* clade. This clade looks to have broken off early, making it a sister group to all other Sylviolids (Alström *et al.* 2006, Fuchs *et al.* 2006, Fregin *et al.* 2012).

The difficulty in accurately positioning *Panurus* within its phylogeny could be driven by its ecology. Jonsson and Fjeldsa (2006) suggest that the taxa within the *Passerida* that 'move around' include many species with wide distributions and large population fluctuations. In addition to a wide distribution throughout Eurasia, the Bearded Reedling populations can fluctuate extensively (See van Turnhout et al, 2010; Wilson and Peach, 2006, and '*Population*' section below for details). These factors may drive genetic bottlenecks and founder events contributing to faster rates of molecular change. When analysis is carried out relative to species undergoing less intense change, the statistical techniques used to construct phylogenies may become obscured (See Bergsten, 2005). In addition, the highly fragmented population structure, coupled with a fast maturation rate in this species, could drive a wide range of divergent genotypes and even faster rates of evolutionary change between distinct populations, masking the origins of this species further. More advanced phylogenetic methods, which consider these factors, may reveal further insight into the evolutionary history of this enigmatic species.

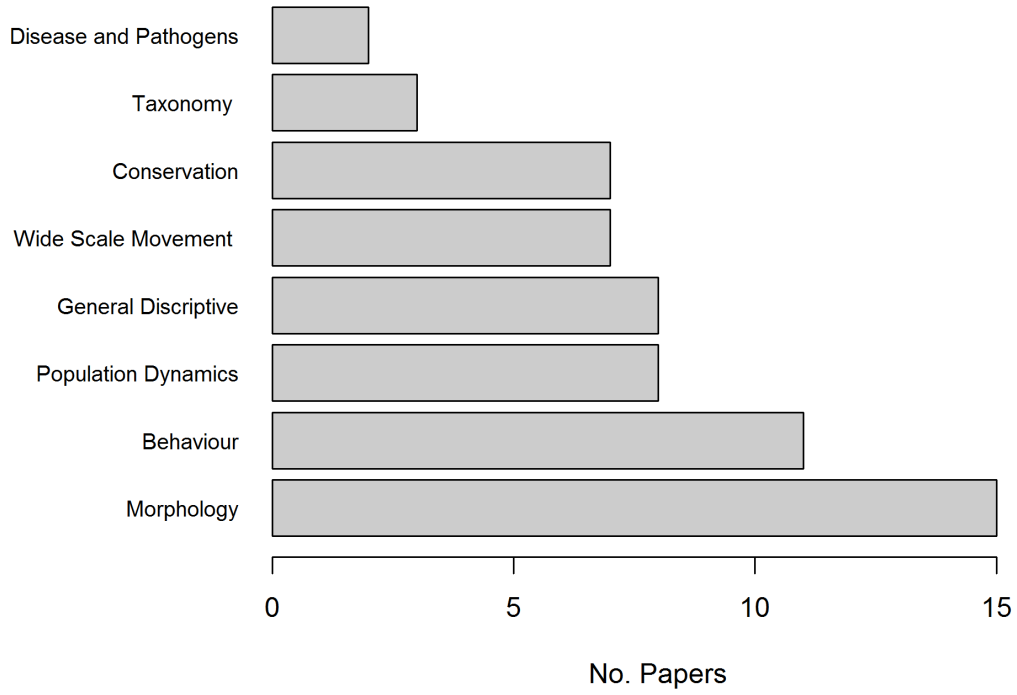


Figure 2.2 – English language research papers written since 1970 with the Bearded Reedling as the main focal species, split into their general research areas. Search conducted using Web of Science online database, on the 21/09/2015 using keywords: "Bearded Tit", "Bearded Reedling", "Panurus biarmicus".

2.4 Morphology

Of the 61 studies directly focusing on the Bearded Reedling, 15 (25%) concerned the distinct morphology of this species (*Figure 2.2*). The males have a greyish head with a prominent black 'moustache' (Svensson 1992), with a long tail and bright orange bill. Females are of a similar size with a long tail, but lack the grey head and beard, being a tawny, light brown. Studies concerning the morphology of this species have explored the moulting patterns, flight feathers and eye colour.

Moult is an integral part of a bird's lifecycle. When mature, feathers are dead structures which eventually become worn and need replaced (Svensson 1992). The Bearded Reedling is one of a small selection of apparently unrelated species that undergoes a full post-juvenile moult. As both adults and juveniles undergo a full moult every autumn, there is no method to distinguish between first-year and adult birds after the end of September (Pearson 1975, Svensson 1992). Pearson (1975) provides an extensive account of the moult patterns of a population on the Suffolk coast. Consistent with many other passerine species, during full moult, most of the feathers are dropped within the time it takes for the primary wing feathers to be completely renewed. Thus, the extent of primary moult is a good indication of moult progress. Pearson (1975) found that young birds begin to moult

between late July and early September, finishing around 50-60 days later. Individuals that fledged later in the year had a reduced time between fledging and beginning their post-juvenile moult, with birds fledging in late June beginning moult 7–9 weeks later, and those fledging in August waiting only 2-4 weeks. Birds that fledged later in the year moulted more feathers simultaneously rather than growing individual feathers more rapidly to 'catch up'. Adult birds completed their full moult by the same process as the juveniles, beginning less variably in August after the breeding season and finishing 45-55 days later (Pearson 1975).

Peiró *et al.* (2006) use this detailed moult information as a platform for their investigation into the changes in wing morphology that occur before and after the complete moult in Bearded Reedlings. They noted that juveniles had significantly larger wings after completion of their post-juvenile moult. They also noted that females had more convex wings than males after moult. Such intraspecific differences in morphology suggest that age groups and sexes may have slightly different implications for space use in this species. More convex wings in females and juveniles may allow more precise manoeuvrability in these individuals, but limit their ability to fly further distances efficiently (Lockwood *et al.* 1998). This may suggest a more sedentary role for these groups in comparison to males (Lockwood *et al.* 1998). The larger length and changes in wing shape of juveniles after moulting has been linked with eruptive behaviour between September and October, where groups conduct high flights over the reedbed, occasionally leaving a site completely (Spitzer 1972, Pearson 1975). The initiation of this behaviour immediately after completion of moult perhaps suggests the need for high quality feathers for flight during potential longer distance, between reedbed movements. In many species, moult patterns are strongly aligned to movement ecology (Pearson 1975, Leisler 2011), with studies of moult offering valuable background for studies of space use.

Romero-Pujante *et al.* (2005) demonstrate the implications of slight changes in feather structure or quality for the movement and habitat use of the Bearded Reedling. The tail lengths of individuals were reduced or elongated experimentally before birds were introduced to an aviary with reeds. Birds with elongated tails showed less variation in which postures they occupied. It was unclear if this avoidance in changing position was due to an increased difficulty in alternating postures or whether the birds had greater control over a single posture. Additionally, individuals with smaller tails spent less time in a 'straddling' position where they grasped a different reed stem with each talon. These experiments demonstrate the importance of the tail as a balancing organ of the Bearded Reedling and clarify how slight changes in feather morphology can alter the ways in which an individual interacts with its habitat.

Such interactions are essential when foraging. The ability to remain agile and access different postures and positions on the reeds will allow the efficient exploitation of food items. During the summer this species is wholly insectivorous. Bibby (1981) shows the importance of slow moving invertebrates such as beetles, caddisflies and snails in the summer diet. These species can easily be picked from stems without the need for aerial catching. Instead of migrating during the winter when insects become scarce in temperate climates, Bearded Reedlings alter their gut morphology to allow them to eat seeds. In *Phragmites* reedbeds these become hyper abundant in September and are available on both stems and in the ground litter into February (Bibby, 1981). The morphology of the Bearded Reedling compliments the ability to 'pick' forage on both slow moving invertebrates and seeds when these sources are available. Any extensive changes in tail length, feather structure or even moult patterns could prevent effective manipulation of this specialist habitat and have consequences for fitness.

While it is clear how feather properties and moult patterns can complement ecology, other morphological characters are potentially less adaptive. Pearson (1966) discuss observations on the iris colour of Bearded Reedlings from Suffolk. They note the presence of a polymorphism in iris colour, with some juveniles having brown eyes which transcend through grey becoming yellow or brown just before the post-juvenile moult, and others (12-18% of the population) having a consistently dark brown eye. The changing brown-yellow eye phenotype can be useful when aging juveniles accurately prior to their post juvenile moult (Pearson 1975). Wilson and Hartley (2007) model this process, and demonstrate the accuracy of model estimates in predicting the hatching dates of birds to within 5-10 days. These accurately aged individuals provide critical insight into the seasonal variation in breeding productivity. Whether this trait is condition dependent or influenced by the diet or environment of the individual needs further investigation.

2.5 Behaviour

The behavioural ecology of the Bearded Reedling, especially surrounding breeding, has been another intensively studied area over the last 50 years (*Figure 2.2*). In their first year, during autumn and winter Bearded Reedlings form lifelong monogamous pair bonds. The selection of a high quality mate during this time will therefore have far-reaching consequences for fitness (Griggio and Hoi 2011, Hoi and Griggio 2012). Bearded Reedlings are non-territorial throughout the year, and so any mate choice decisions will be based on the quality of the individual rather than the resources they may hold (Hoi 1997). High levels of extra-pair copulations have been also noted (Hoi 1997, Hoi and Hoi-Leitner 1997), suggesting that even as monogamous adults the ability to identify high quality extra-pair partners offering the greatest indirect genetic benefits will have a role in breeding biology.

Beard length is the major signal of quality in male Bearded Reedlings. Hoi and Griggio (2008) show that beard length acts as an honest signal during male-male agonistic interactions and is positively selected for by females. They investigated the role that beard length had to play in male-male interactions by releasing two males simultaneously into a chamber with a single food source and recording the outcomes of agonistic interactions. In 80% of these experiments the dominant male had a significantly longer beard. They then elongated or reduced the size of the beards of males with similar biometrics and noted how much time a female spent with these manipulated individuals when given the choice. Females spent significantly more time with the males with elongated beards. This trait, based on melanin, therefore plays a duel roll in the social interactions of this species. It acts as a signal that females can use to assess male quality and signal of strength during male-male interactions.

Romero-Pujante *et al.* (2002) note the long tail in both male and females, and suggest that, in addition to its important role in habitat use, it could also be product of sexual selection. Males have slightly longer tails than females and when placed in a choice chamber, females chose to spend more time and exhibited sexual behaviour in front of males with longer tails. Direct sexual selection was, therefore, most likely the driver of the male's long tail. When reversing this experiment, males did not show strong selection for females with the longest tails, but did choose controls over reduced tailed females. The long tail in females is therefore potentially a by-product of stronger sexual selection processes in males. Alternatively, males may not always choose the highest quality female, with the longest tail, due to the increased participation of higher quality individuals in extra pair copulations (Hoi and Hoi-Leitner 1997). Sexual selection clearly has an important role in this species, with behavioural studies allowing strong insight into the mechanisms surrounding this evolutionary process.

Recent studies have shown that many temperate, monogamous song birds seek extra-pair copulations during the breeding season, resulting in a high proportion of offspring within a nest not being genetically related to the male providing the parental care (Westneat and Stewart 2003, Akçay and Roughgarden 2007). Female Bearded Reedlings have evolved conspicuous methods to assess the quality of potential extra pair partners. They undertake 'chase-flights', which occur most frequently during nest building (Birkhead and Hoi 1994, Hoi 1997). The female approaches a male and encourages him to mount. When this is attempted, however, the female resists and flies above the reeds calling. This call attracts other nearby males who are notified of her fertility and proceed to join in the chase. Eventually the female flies lower, among the reeds, turning sharply. On completion of the chase flight, the male that has kept up with her most effectively is permitted to

copulate (Birkhead and Hoi 1994, Hoi 1997). The chase selects the most agile male and by allowing this copulation the female gains indirect fitness advantages. Hoi (1997) experimentally show that females carry out more chase flights when they are fertile and in the presence of other males. Both these factors support the suggestion that chase flights are means for females to entice males into competing, allowing an efficient assessment of male quality.

Hoi and Hoi-Leitner (1997) note that females paired to males with longer beards participate in a reduced number of extra pair copulations. In addition to the quality of the male the effort or investment that the male puts into the pair bond may reduce the number of extra pair copulations the female participates in. Hoi and Griggio (2012) show that, when a monogamous pair are placed in a chamber with another individual they adjust their investment into the pair bond. When a high quality female is present, the paired female initiates more contacts with her partner. Similarly, the male will invest more into the pair bond if another male is present.

The complex extra-pair processes in this species may also have an important influence over space use (Hoi and Hoi-Leitner, 1997). Bearded Reedlings are non-territorial and form loose colonies when breeding. However, some pairs may also nest in solitary, up to several hundred metres from other nests. With use of molecular techniques, Hoi and Hoi-Leitner (1997) noted that there were higher levels of chase flights and extra-pair copulations in colonies, with 29.5% of nests in colonies having offspring fathered by an extra-pair male. No chase flights or extra-pair copulations occurred in solitary nests. While male quality, which was based on the size and condition of the individual, did not change between colonial and solitary breeding males, higher quality females were consistently found in colonies. It was also noted that colonial nests had similar rates of predation to solitary nests, suggesting colonial birds not receive any traditional benefits from remaining gregarious, such as the dilution of predation. A major benefit of colonial breeding in this species, therefore, could be the ability to gain an increased number of extra-pair copulations. High quality females will gain fitness benefits by having a wider selection of males, allowing the production of more variable offspring. Low quality females, however, may nest solitarily to avoid the costs, such as brood parasitism, increased intrasexual competition and the tendency of males to chase other females, of living in colonies. Behavioural processes may therefore be critical when shaping even the most fundamental aspects of space use, such as coloniality, in this species.

Birkhead and Hoi (1994) investigated whether extra pair copulatory behaviour influenced the morphology of the sexual organs or the properties of the sperm in this species. Consistent with other more promiscuous species, male Bearded Reedlings had heavier testes than would be expected of a bird with this body size. This could facilitate the production of more sperm, suggesting

a high copulation rate. On dissection, they also noted the unique structure of the cloacal protuberance in the males. When squeezed it moved away revealing a phallus like structure. Large cloacal protuberances in other male passerines allow storage of sperm, but the exact role of this structure in the Bearded Reedling remains unclear. Females also have wide cloacas that have a high rate of sperm loss after copulation and are limited on how many sperm they store (Sax *et al.* 1998). Sax et al (1998) suggest the high rate of sperm loss caused by this limit could be adaptive. If a female can quickly lose her monogamous partner's sperm after copulation it makes it more likely that any subsequent extra pair copulations will result in fertilisation.

2.6 Population Dynamics

Understanding the fine-scale behavioural processes operating during breeding provides important background when observing the dynamics of full populations. However, in order to study population dynamics and trends, suitable methods for monitoring must first be established. Reedbeds are dense and often inaccessible habitats, limiting the effectiveness of traditional population monitoring techniques (Haukioja 1968) when surveying Bearded Reedlings. Poulin *et al.* (2000) investigate the efficiency of point count and mist netting techniques for studying bird abundance and assemblage in reedbeds. Both techniques provided results with a similar degree of accuracy. However, with decreasing sampling effort species with the highest variance were often not accurately estimated. The Bearded Reedling showed high variance due to its gregariousness, sometimes being abundant when netting or during counts, and other times being completely absent. When studying this species, such variance must be accounted for by increasing the survey effort. A means to increase encounters with this species is through use of tape-lures (Surmacki 2003), which can encourage birds into nets or to reply during counts. While, alternatively, line transects may also be useful when observing changes in abundance in relation to habitat gradients (See Moskát and Baldi 1999), point counts from a raised location within the reeds may allow more observations, accurate distance estimation and mitigate some of the difficulties caused by the inaccessibility of reedbeds. Despite these methods, studies unanimously agree that monitoring techniques for this species remain unsatisfactory, with the further development of adequate methods being an important area for further research.

One property common to many Bearded Reedling populations is the tendency to show marked fluctuations in numbers (Pearson 1975, Bibby 1981, Wawrzyniak and Sohns 1986, Elzen 1993, Wilson and Peach 2006, Surmacki and Stępniewski 2007, Beemster *et al.* 2010). Ringing efforts in the Tay Reedbeds in east Scotland resulted in 373 newly trapped birds in 2004, around 30% of the UK's total ringed population, yet despite similar effort in the following season, only 40

new birds were trapped (Hatton 2008, Malzer and Spinks 2015). Similarly, Dutch populations in Zuidelijk, Flevoland, saw initial highs of 7000 breeding pairs in 1975, but numbers had dropped dramatically to around 800 by 2000 (van Turnhout *et al.* 2010). These large fluctuations make it difficult to establish clear population trends in this species at both a local and wide-scale.

Winter mortality looks to be a key factor driving the numbers of Bearded Reedlings at a local scale. In Leighton Moss, England, extensive winter flooding blocked access to seeds within the litter layer, resulting in the mortality of 94% of the Bearded Reedling population (Elzen 1993, Wilson and Peach 2006). Surmacki and Stepniewski (2007) suggest that local climatic conditions have a strong influence on Bearded Reedling populations, and that a warming climate may allow earlier breeding, facilitating population increases and expansion. However, in many areas climatic change may also cause increases in the occurrence and intensity of severe weather events, such as flooding or storms. These accounts for fluctuations are site specific and to date there has been no research integrating population dynamics over a wide-scale.

At the opposite extreme, Bearded Reedling populations may experience highly productive years. This is facilitated by this species' high reproductive output which may be a means to cope with winter mortality (Wilson and Peach 2006). Breeding normally begins by the end of March, after which this species can have multiple broods into August (Bibby 1983). The tendency to rear up to four broods in a single season is common, and with an average of five young per brood (Surmacki *et al.* 2003), exceptional numbers of individuals can be recorded in the autumn (Bibby 1981, 1983). This may be especially apparent in mild years when high early spring temperatures might both allow birds to begin breeding early, and increase brood success throughout the season (Surmacki and Stępniewski 2007).

2.7 Conservation and Ecology

Studies of the interactions between Bearded Reedlings and their local environment may reveal further insight into the mechanisms underlying population dynamics. Reedbeds can vary widely both over space and time. Studying the occurrence of birds in changing microhabitats within the reedbeds, and the attributes of these areas, may allow conclusions to be drawn about important ecological features of reedbeds. Baldi and Kisbenedbk (1999) and Moskát and Baldi (1999) both note the importance of an edge effect in the distribution of birds throughout the reedbeds. Eight out of 14 species studied showed a distribution affected by proximity to the edge of the reedbed, with the Bearded Reedling showing a strong preference for the first five metres of the reedbed. This was potentially due to increased invertebrate levels in these areas (Hoi *et al.* 1995), but it remains

unclear whether this effect persists through the winter when seeds offer the most effective foraging. Bearded Reedlings have also shown a preference, when nesting, for the boundaries between the reeds and small pools (Hoi, 1989), this could be due to the slightly reduced predation rates noted by Baldi and Kisbenedbk (1999) or the easier access to aquatic invertebrates.

When investigating the local distribution of a Dutch population of Bearded Reedlings, Beemster *et al.* (2010) note the additional importance of heterogeneity in the age structure of reeds. Over time, with many layers of new growth, old strands of reed become dense and dry. These areas provide thick reed stems that can act as important nest foundations (Hoi, 1989). Observations of breeding Bearded Reedlings have shown distant parental foraging flights of as far as 500 metres (Poulin *et al.* 2000, Beemster *et al.* 2010). This suggests that, while suitable for nests, old reed is not necessarily the most effective foraging patch. Beemster et al (2010) showed that open, younger, reeds that had been recently grazed by geese constituted the main feeding areas. These areas were found to have the highest invertebrate abundances but this effect has not been replicated in other sites (Valkama *et al.* 2008). Thinner stems in early successional areas, allowing easier access when foraging, have been suggested as an alternative reason for directed foraging in these areas (Trnka and Prokop 2006). These areas also offer effective winter foraging, having increased seed abundances (Beemster *et al.* 2010). Fluctuations in water levels and grazing, should ensure a degree of heterogeneity in reed ages. However, reed management could also have an important role in maintain variation in age structure.

Reeds can be cut, rolled or burned, with harvesting of stems for use as thatch the major incentive for reedbed management in Europe (Poulin and Lefebvre 2002, Valkama *et al.* 2008). Studies have investigated the impacts of management on an array of different plants and animals, and revealed wide variation between sites and species. Valkama *et al.* (2008) conducted a meta-analysis of the available literature. Reed cutting increased the diversity of plant species throughout the reedbeds and changed the structure of the reeds themselves. Reeds grew back more densely but at a lower height in managed areas. The diversity and abundance of invertebrates showed wide variation between studies. Overall, there was an immediate decrease in the abundance and diversity of invertebrates at managed sites. However, trends were species specific with groups such as the Acarina, Isopoda and Homoptera, all which may have relevance as prey for the Bearded Reedling, being more abundant in managed areas. In contrast Poulin and Leverbvre (2002) suggest that managed areas have an increased food index based on invertebrate samples. However, changes in invertebrate abundance and assemblage only occurred after management had been implemented on a given site for over four years.

The meta-analysis revealed that overall bird abundance was lower in managed areas. The lack of reed as a key breeding habitat prior to new growth is likely the major reason for this (Graveland 1999). A compromise may therefore be found in mosaic reed cutting, where small patches of reed are cut and areas of old reed maintained. This is often conducted purely for conservation, preserving the long term integrity of the reedbed and providing heterogeneity in the age structure of reeds (Hawke and Jose 1996). This form of cutting preserves suitable patches of old reed in which breeding birds can nest. Trnka *et al.* (2014) also suggest that cut areas in a mosaic can be immediately re-colonised by invertebrates from neighbouring uncut patches. Despite the wide implementation of this technique, little research has been conducted on the interactions of reed specialist birds with mosaic reedbed management. Indeed, all previous studies of habitat selection in reed passerines have been conducted at the population level, using abundance as a proxy for preference. Future studies should consider individual level space use which may reveal the fine-scale interactions between reed management and specialist reed species. Such information could be critical for the continued enhancement of reedbed sites.

2.8 Wide-scale Processes

While understanding the ways in which populations behave within a single reedbed is important for local-scale conservation, studies of wide-scale, between reedbed, processes may provide further insight. Bearded Reedlings exist throughout most of Europe as a fragmented metapopulation. In many cases, single reedbeds exist in isolation, large distances from other patches. Generally, this species is considered sedentary and resident, with few movements being recorded, especially in lower latitude regions (Marin and Marchesini 1994, Peiro *et al.* 2006). When combined, these factors may lead to low gene flow between populations, and potentially inbreeding. Marin and Marchesini (1994) explore this within an especially isolated population of Bearded Reedlings near Venice, Italy. They find no evidence of inbreeding when using DNA fingerprinting to analyse the degree of relatedness within the population. Indeed, the levels of heterozygosity noted were only possible if extensive immigration was occurring, despite the fact that during surveys, no movements into or out of the population were observed.

Bird ringing data offer a means to study the tendency for birds to move at wider distances, with many of the Bearded Reedling studies offering accounts of ringing recoveries and descriptions of movement patterns. Generally, lower latitude regions remain sedentary throughout the year, with few ringing recoveries occurring beyond 5km (Marin and Marchesini 1994, Peiro *et al.* 2006). Surmacki and Stepniewski (2003) suggest a degree of seasonality in the movements of a fragmented population in Poland, demonstrating the tendency for birds to move to smaller, low breeding quality

reedbeds during the winter. Dürr *et al.* (1999) report longer distance, directional, movements of Bearded Reedlings ringed in Germany towards the south west during the autumn, from which a high proportion of birds return in the spring. These are further summarised in Wawrzyniak and Sohns (1986) and Elzen (1993). Similar seasonal movements of Bearded Reedlings from Suffolk in England are detailed in Pearson (1975) and Cramp and Perrins (1993), with autumnal movements occurring in September. Despite this no study offers a combined, wide-scale analysis of the movement strategies of the Bearded Reedling, with such a study being necessary when understanding the variation, and flexibility, in the movement of this species.

2.9 Conclusion

The published literature regarding the Bearded Reedling provides insight into many aspects of this species' biology. Its phylogenetic history remains unclear, further molecular research conducted over a range of related species is needed to confidently establish the taxonomic origins of this species. Other features of the biology of the Bearded Reedling, including; its morphology, behaviour and the dynamics and movements of populations look to be linked to its complete dependence on reedbed habitats. While some aspects of the ecology are well developed, due to the difficulty of observing Bearded Reedlings in the wild, little information is available on local, individual-scale space use of this species. Further information on local-scale space use throughout the year could inform reedbed management, and help conservationists enhance key reedbed sites for this species. Research concentrating at the wider-scale may also be critical for conservation. Such studies should seek to integrate the movement patterns of this species over a wide-scale, aiding our understanding of colonisation events and seasonal movements in this species.

Chapter Three

Spatially explicit capture-recapture methods; estimating the density of an elusive reedbed Passerine

Iain Malzer, Stewart White, Barbara Helm

3.1 Abstract

Rare and elusive species are often dependent on inaccessible habitats. These species often suffer from under-recording and a lack of monitoring making it difficult to establish how they may react to environmental change. Thus, methods that can cope with limited accessibility and detectability when estimating animal abundance are critical for informed conservation. Capture-recapture techniques are often used to monitor rare and elusive species, allowing traps to be set in accessible areas of the habitat and removing the need for direct field observations. Recently, the incorporation of spatial information into capture-recapture models has allowed estimates of abundance which are unbiased by the spatial organisation of the population and explicitly defined over a geographic region. In this study we use spatially explicit capture-recapture (SECR) methods to estimate the population size of a rare and elusive Passerine, the Bearded Reedling in a nationally important site for the UK. Throughout 2014, we collect capture-recapture data using mist-netting and ringing and augment these with simultaneously collected radio-telemetry information. This protocol allowed estimates of abundance from SECR models for both: adults during the 2014 breeding season, and all birds throughout the full year. Our estimates of 134 (101, 176) adult Bearded Reedlings during the breeding season, and 3075 (2625, 3602) unique birds throughout the full year, demonstrate the high significance of this site for the Bearded Reedling, and emphasise the value of contemporary SECR modelling techniques when estimating the abundance of elusive species.

"Who would swallow such a change? So why not keep the accepted name of Bearded Tit? I am unsure why the name changers have not had a go at the Long-tailed Tit on the same grounds of it not being a proper tit. Long-tailed Scrubling? Heaven forbid!"

Colin J. Bibby, 1983, British Birds 76

3.2 Introduction

Animal populations face a number of threats; from wide-scale, gradual climatic change (Thomas *et al.* 2004), to local-scale habitat modification or destruction (Fischer and Lindenmayer 2007). Such threats may be especially pertinent for rare and elusive species, which are often highly dependent on specific habitats with the consequence that even slight changes in their environments could have severe impacts for the population as a whole (McKinney 1997, Colles *et al.* 2009). In order to fully understand the effects of environmental change on species, adequate and effective monitoring techniques are imperative, a key factor of which are appropriate methods with which to estimate population size. Unfortunately, rare species, while being in need of close monitoring programs, tend highly elusive and often occupy inaccessible habitats, making them some of the most difficult species to census (Thompson 2004).

A broad range of techniques have been developed to allow estimation of animal abundance (Schwarz and Seber 1999). While these are often species specific, general methods include monitoring changes in site occupancy (Royle and Nichols 2003), surveying tracks or other indices of animal presence (Stephens *et al.* 2006), counting individuals while controlling for dectectability (Buckland 2006) and capture-recapture techniques (Otis *et al.* 1978, Borchers 2012). As capture-recapture methods can be undertaken by setting traps remotely and avoid the need to intensively survey over difficult terrain, they offer an effective means to monitor elusive species in inaccessible habitats (for example Tøttrup *et al.* 2004; Karanth *et al.* 2006; Blanc *et al.* 2013). Traditional capture-recapture methods involve the capture and unique marking of individuals from the studied population over several occasions. Trapping methods range from bird mist-netting and mammal trapping to modern, non-invasive, sampling involving camera traps (Sollmann *et al.* 2013) or genetics (Lukacs and Burnham 2005). The ability to infer abundance from such data has had a long history (Peterson 1896, Lincoln 1930), with more modern statistical techniques allowing estimation of parameters such as survival between sampling periods, and accounting for individual heterogeneity or behavioural changes in capture probability (Otis *et al.* 1978, White and Burnham 1999, Pollock 2012).

Recently, spatial information, which is an intrinsic component of many capture-recapture datasets, has been incorporated explicitly into models in order to better define abundance estimates (Borchers 2012, Efford and Fewster 2013, Royle, Chandler, Sollmann, *et al.* 2014). Spatially explicit capture-recapture models are informed of the location of each trap throughout the study region and the spatial capture history of each specific individual. With this information, animal activity centres can be estimated, with the location of this centre determining the individual's probability of capture

in a given net. This modelling process has gained support in its ability to offer estimates of population density which are unbiased by the spatial organisation of the population and potential changes in capture probability throughout space (Obbard *et al.* 2010, Blanc *et al.* 2013, O'Mahony *et al.* 2014, Royle, Chandler, Sollmann, *et al.* 2014, Sarmento and Cruz 2014). Further, in non-spatial models, density is a derived parameter based on the estimated population size over an unclear, and often subjective, sampling area. Another advantage of SECR models is the ability to explicitly define a specific sampling area within the models, over which direct estimates of density can be integrated (Borchers 2012, Efford and Fewster 2013). Total population size can then be inferred from density estimates over a well defined geographic region.

In parallel to the clear advances in the analysis of capture-recapture data, techniques for the collection of direct spatial information from animals have also markedly progressed (Kays *et al.* 2015). Radio and satellite telemetry methods allow the location of individuals to be monitored directly over time, with clear value in studies of resource selection (Manly *et al.* 2002), physiology (Signer *et al.* 2010), migration (Qian *et al.* 2009) and population dynamics (Morales *et al.* 2010). This information may also make a valuable contribution to the estimation of population abundance. When united with spatially explicit capture-recapture methods, telemetry data may be used to further inform models with spatial parameters (Sollmann *et al.* 2011, Royle *et al.* 2014, Efford *et al.* 2016) such as direct measures of animal activity centres or home ranges. This augmentation of capture-recapture methods with direct spatial data may be especially important when trapping datasets offer limited recaptures from which only sparse spatial information can be gathered. As the capture-recapture monitoring of rare and elusive species often results in low numbers of recaptures, these methods should be explored when estimating the abundance of rare species.

The Bearded Reedling, *Panurus biarmicus,* is a reedbed Passerine, completely resident to local reedbed habitats. These unique wetlands, which constitute vast single-species stands of Common Reed *Phragmites australis,* have declined over the last century, and are becoming more restricted geographically due to wide-scale drainage, infrequent colonisation of new sites and reed dieback (Everett 1989, Hartog *et al.* 1989, Gigante *et al.* 2014). While the Bearded Reedling is classified as 'of least concern' on the IUCN's red list due to its wide range (BirdLife International 2014), its dependence on reedbed sites drives a highly fragmented population structure, with key populations clustering around large reed stands. In many of these, monitoring has revealed the tendency of these birds to undertake wide population fluctuations, the causes of which may be related to winter weather (Pearson 1975, Bibby 1983, Wilson and Peach 2006, Surmacki and Stępniewski 2007). In addition, these sites are often subject to extensive anthropogenic

management, which may involve dramatic local alteration of the habitat during commercial reed harvesting for thatch and biomass (Hawke and Jose 1996, Poulin and Lefebvre 2002). When combined, the general loss of reedbeds, climatic change and local-scale habitat modification may have wide-reaching consequences for reedbed specialists such as the Bearded Reedling. In order to monitor these consequences, adequate methods with which to estimate abundance are imperative.

However, in practice, such estimates are difficult to obtain. Reedbeds can be inaccessible, being both frequently inundated and consisting of dense reed stems (Haukioja 1968). Further, these birds can be elusive and difficult to see within reedbeds, tending to remain low in the stems (O'Sullivan 1976, Campbell *et al.* 1992). Thus, while conventional survey approaches such as transects or point counts can offer useful relative comparisons between sites (Surmacki and Stepniewski 2003, Beemster *et al.* 2010) they offer minimal data with which to estimate overall abundance (O'Sullivan 1976, Poulin *et al.* 2000, Surmacki 2003). In addition, the lack of territorial behaviour in this species has limited the use of territory mapping techniques, which have proven successful for several other reedbed species (van Turnhout *et al.* 2010). Capture-recapture methods may therefore offer the most useful abundance estimations for this species. Mist-nets can be positioned in accessible areas and are not dependent on direct sightings. Wilson and Peach (2006) successfully implement a long-term capture-recapture study when monitoring Bearded Reedlings at a site in northern England, using non-spatial methods to estimate adult population size at around 100 individual adults. Further mist-netting studies have proven successful when investigating habitat use (Poulin *et al.* 2002, Trnka and Prokop 2006) and reed management (Poulin and Lefebvre 2002) for this species.

In this study we use spatially explicit capture-recapture methods to estimate the population size of Bearded Reedlings in the Tay Reedbeds, Scotland. This is the largest reedbed on the British Isles, consisting of 4.1km^2 of uninterrupted Common Reed. Long-term ringing data suggest the colonisation of the Tay in around 1992. Peach (2000), provides population estimates at this site, conducting a high effort capture-recapture study and suggesting an abundance of 190 breeding adults in 2000 using non-spatial closed population estimates. However, there remains no subsequent analysis of population sizes at this important site, which may be useful when highlighting population trends. Further, fast tidal movements and large ditches limit accessibility when surveying at this site, with only a small number of areas offering effective mist-netting locations. Thus, spatial methods, unbiased by incomplete coverage and explicitly bounded to the reedbed area, could offer the most realistic estimates of abundance.

We offer a subsequent analysis of the abundance of Bearded Reedlings on the Tay Reedbeds. We demonstrate a protocol, undertaken during 2014, that allows population estimates to be constructed from spatially explicit capture-recapture techniques. Capture-recapture data are collected using mist netting and ringing techniques. However, where spatial data from the mist netting protocol are sparse, we augment the models with location data collected from a sample of radio-tracked individuals. Using this protocol we provide estimates at two levels: for adults during the breeding season, and all birds throughout the full year. Estimates of adult birds during the breeding season offer a useful indication of breeding numbers within a closed population. However, as Bearded Reedlings are highly prolific and have the tendency to undergo dramatic population fluctuations (Wilson and Peach 2006), an estimate of the total number birds occupying the reeds throughout the full year offers further insight into the importance of this site. We aim to provide the most up to date, accurate estimates of abundance of Bearded Reedlings on the Tay, over a well defined sampling region to provide more insight into the true numbers of this elusive species in the UK and offer a useful resource as decisions are made on the future management of the Tay Reedbeds.

3.3 Methods and Materials

3.3.1 Capture-Recapture Protocol

The Tay Reedbeds form a narrow fringe along the northern bank of the Tay Estuary varying in width between 150 to 500m. Sampling and population estimates were conducted in a 2.3km^2 stretch of the reed between Tay Lodge in the west (56° 22.70'N, -3° 12.432'W) and Kingston (56° 25.89'N, 3° 7.31'W) in the east (*Figure 3.1*), as previous surveys suggest this section hosts the highest numbers of Bearded Reedlings (Peach 2000).

Population estimates were based on a mark-recapture protocol using mist netting and bird ringing techniques. This protocol was implemented throughout the full year in 2014. Intermittent stone dykes extending out from the land edge of the reedbed to the river edge offered access to the centre of reeds. At four of these dykes, spaced on average 2km apart, mist nets were erected at least once a month. These four mist netting dykes were named "Tay Lodge", "Seaside", "Powgavie" and "Kingston" (*Figure 3.1*). Within each site 18m long, 2.75m high, mist nets were erected in designated locations. In total, 44 individual net locations were designated throughout the reedbed: 8 at Tay Lodge, 19 at Seaside, 6 at Kingston and 11 at Powgavie. As the dykes were linear, in most cases the cluster of mist nets within each site formed a continuous line. However, at Powgavie the narrow width of the reed meant a clustered approach was more appropriate (*Figure 3.1*). Within a site, mist-nets were on average 20m apart. Each mist net was given a unique label allowing its specific location to be identified.

In every month throughout 2014 from January to December, each of the four mist netting sites were visited at least once and a number of nets opened at dawn for five hours. The number of nets opened in each site during a single visit was left to the discretion of the coordinating ringer, with the availability of personnel meaning that all net locations were rarely active at the same time. To cope with this variation in effort ringers recorded exactly which nets were opened on each visit, information that was subsequently included in the population models. This information would also control for occasions when the net may be active for more than one session in a month.

Upon capture, each individual Bearded Reedling was fitted with a standard metal BTO leg ring that had a uniquely identifiable code. Additionally, a note was made of the exact net from which each individual was extracted. Standard biometrics, including age and sex following Svensson (1992), were also recorded prior to the release of each individual back into the population.

During the April sampling, ten randomly selected adult birds from the Seaside site, and six from Powgavie, were fitted with radio-trackers. Radio transmitters (0.4g PIP3 single celled tags;

maximal dimensions 7mm x 7mm x 4mm) were sewn onto a square of cotton cloth (surface area 1cm^2). A patch of feathers on the central upper back of the bird was then trimmed before the cloth was glued to this area using latex based eyelash adhesive. The tags were 0.025% of the mean weight of all the birds tagged over the study (15.5g) and never exceeded 0.03%. Tags were expected to remain attached for between from mid April to mid May. Birds were then intensively tracked by triangulating the position of the radio signal from the bank of the reedbed using two Biotrack SRX600 VHF radio receivers with flexible Yagi antennas. Simultaneous bearings were collected by two field researchers standing between 50 and 100m apart. Preliminary information was collected on the accuracy of the locations estimated from triangulation by leaving transmitters in known positions throughout the reedbed and comparing these with the estimates. 15 trials suggested the transmitters were accurate to with 12.5m when three bearings were taken. This telemetry dataset offered a means to augment population models during the breeding season (see statistical analysis section).

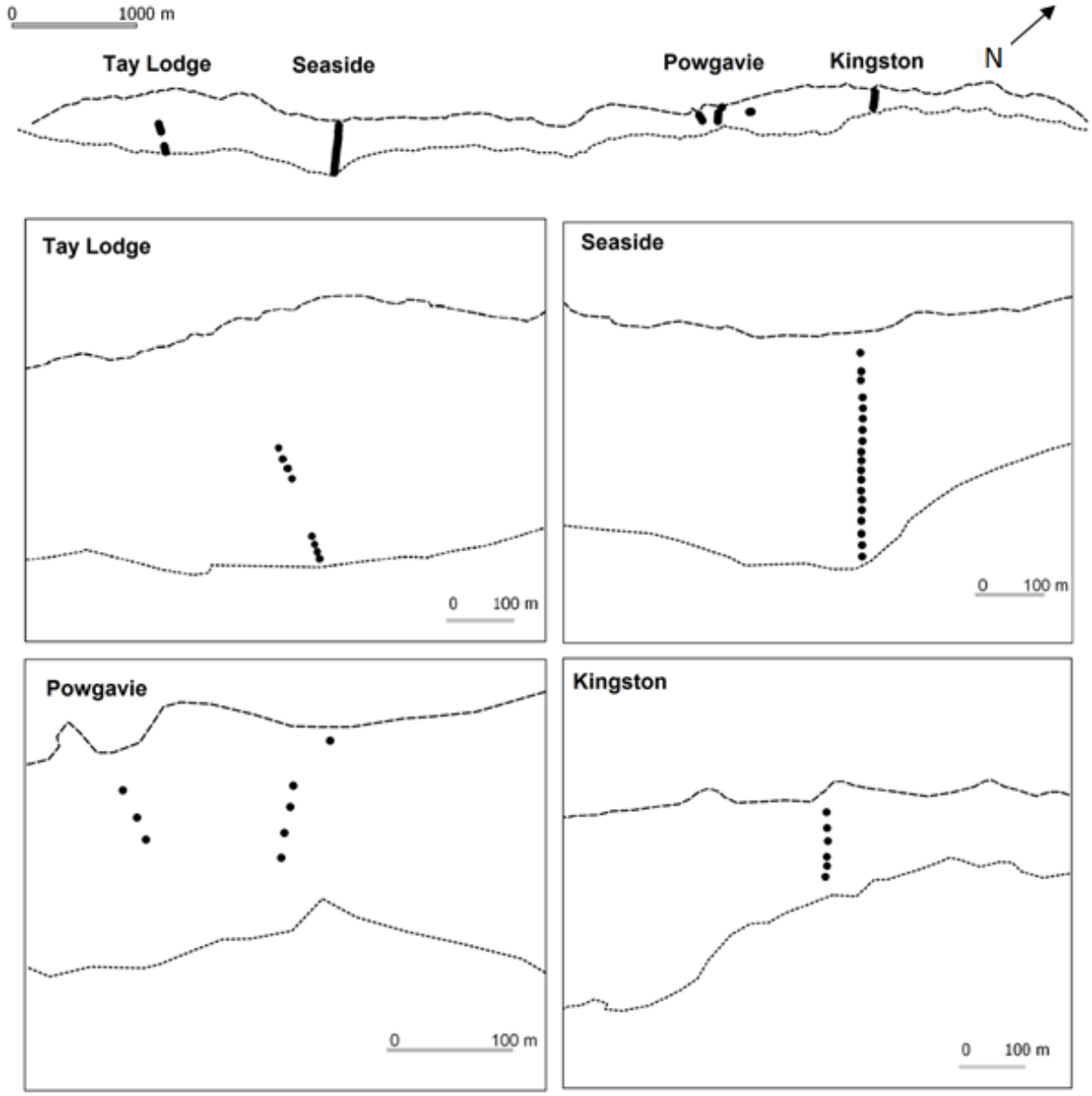


Figure 3.1 – Mist netting locations on the Tay Reedbeds. The top panel shows the four main mist netting sites, while the lower panels show the specific layout of nets within each site. Solid black circles represent the mist net locations, dashed line is the land edge, dotted line is the river edge. The arrow points North.

3.3.2 Statistical Analysis

We analysed population size at two levels during 2014: for adult birds during the breeding season, and for all birds throughout the full year. The breeding season data included all captures of adult birds between April and August, which corresponds to the breeding season of this species (Cramp and Perrins 1993). All adults captured during the breeding season were in clear breeding condition and assumed to be undertaking breeding activity. In the full year dataset, both juveniles and adults, from January to December were included as juveniles cannot be differentiated from adults after the post juvenile moult in September. In both levels of analysis all data from a single month are pooled and each month considered a single sampling occasion, resulting in five occasions during the breeding season and 12 occasions in the full year.

We estimated population sizes using spatially explicit capture-recapture (SECR) methods (Borchers 2012, Efford and Fewster 2013, Royle, Chandler, Sollmann, *et al.* 2014). SECR models consist of an observation model and a state model. The observation model describes the decline in probability that an individual will be captured in a specific trap, as the individual's activity centre, which can be interpreted as the centre of the animal's home range, increases in distance from the trap (Efford and Fewster 2013). These take the shape of a detection function, normally described by two parameters: g0, the probability of capture at zero distance from the trap, and σ, the scale over which the probability of detection declines. Using the spatial capture histories for each individual the location of the activity centres can then be estimated. The state model then describes the distribution of animal activity centres throughout the sampling region by integrating over a pre-defined habitat mask. This is modelled as a Poisson point process with the sole parameter, intensity, describing the density of animal activity centres over the defined geographic region (Borchers and Efford 2008, Borchers 2012). Density surfaces can also be inhomogeneous, and constrained to describe directional trends or relevant environmental covariates (Borchers and Kidney 2014).

We estimated spatially explicit capture-recapture parameters in the maximum likelihood framework of R package secr (Efford 2015). The likelihood function was evaluated at points spaced 50m apart over a habitat mask that covered the studied section of the reedbed (as shown in *Figure 3.1*). The mask ensured that density was modelled only within the boundary of the reedbed. As mist-nets allow the capture of multiple individuals in each occasion, but prevent the same individual being captured in several traps, we defined our traps as "multi-catch" traps when estimating likelihood. Further, in all models we incorporated a measure of netting effort. We did this by informing models of the number of times each net was active in a given occasion (Efford *et al.* 2013). This formed a usage matrix with zero values for nets which remained inactive during a given

occasion, and a continuous integer for active nets informing of the number of times the net was active in the occasion. In including a measure of known variation in effort, we increased model fit, and reduced potential confounding effects (Borchers and Efford 2008, Efford *et al.* 2013). As SECR models assume the population is closed we tested each data set for violations in this assumption using the closure test of Stanley and Burnham (1999).

In the adult breeding season dataset there were few spatial recaptures (see results). Thus, we provided further spatial information with location data from the sample of radio-tracked individuals. As the radio-tracked individuals were a random sample of the same population sampled during the capture-recapture study we considered telemetry data as 'dependent', allowing them to be directly incorporated into the likelihood estimation process (Efford *et al.* 2016). In doing this we informed the models of the home range sizes of a sample of individuals, and how far they tended to move in relation to their estimated centres of activity. More explicitly, we informed the parameter σ within the observation model with the scale of movement during the breeding season, reducing the variance in this parameter. We did not include telemetry data when modelling the full year dataset as the number of spatial recaptures was higher, making the additional information added by telemetry data negligible at this level of the analysis (Efford *et al.* 2016).

The same suite of SECR models were fit independently to the adult breeding season dataset and the full year dataset. These allowed the modelling of individual heterogeneity and temporal variation in both the probability of detection (g0) and the scale of movement (σ) parameters. *Table 3.1* provides the notation and a description of the suite of models fitted. Further interactions or covariates caused convergence problems when maximizing the likelihood and so only simple models were considered. The most parsimonious models, from which population estimates were drawn, were selected using AIC methods.

Model	**Description**
g0~1, σ~1	Probability of detection and scale of movement constant between occasions.
g0~T, σ~1	Probability of detection estimated for each occasion; scale of movement constant between occasions.
g0~1, σ~T	Probability of detection constant between occasions; scale of movement estimated for each occasion.
g0~T, σ~T	Probability of detection and scale of movement estimated for each occasion.
g0~B, σ~1	Behavioural response in probability of detection after first capture where probability of recapture can either increase or decrease after initial capture; scale

of movement estimated for each occasion.

Table 3.1 – SECR observation models fit to the breeding adult and full year Bearded Reedling capture-recapture datasets.

We also separately modelled changes in density throughout the reedbed as an inhomogeneous Poisson point process. Due to problems in convergence the observation models were held constant when modelling geographical variation in density. Thus, density surfaces are only used to highlight potential changes in density throughout space, rather than estimate population sizes. We modelled the distribution of animal activity centres as a function of continuous spatial trends in either the east to west (X) axis or north to south (Y) axis. We geographically rotated the original reedbed polygon so that the main axes of the reedbed correspond to these directions (as in *Figure 3.1*). We then modelled density by treating X and Y co-ordinates as continuous covariates. As we did not expect linear directional trends, the models were fit with high order terms. Fitting high order polynomial terms can often cause problems in the numerical convergence, thus, we used regression spline smooths which are a flexible alternative (Borchers and Kidney 2014) and can be implemented in secr through R Package mgcv (Wood 2006). We modelled directional trends in the east to west direction allowing up to five knots in the smoothing function, and up to three knots in the north to south direction. A higher maximum number of knots was permitted on the east to west axis as this was longer in distance relative to the north to south axis and more likely to require a complex shape. Models with flexible density surfaces were compared to null models with homogeneous density surfaces using AIC methods. The most supported models were used to predict a density surface throughout the study region.

3.4 Results

3.4.1 Adults during the breeding season

Over the breeding season of 2014, from April until the end of August, a total of 157 mist-nets were active, with all 44 trap locations being active at least once. The average number of nets opened per month was: 12 at Powgavie, 6 at Kingston, 8 at Tay Lodge and 15 at Seaside. 96 individual adult Bearded Reedlings were captured over this period, with only 10 being recaptured again during the breeding season. The recaptures are depicted in Appendix I. 53 captured birds were males, 47 were females. Closure tests suggested the population was closed during this period ($z = -0.95$, $P=0.17$). In order to increase spatial information within the models, we added dependent telemetry data from 16 individuals. These individuals offered on average 71.8 relocations (range: 19 – 105) with which to inform the scale of detection parameter, σ. *Table 3.2* details the parameters estimated by the spatially explicit capture-recapture models. The model which gained overwhelming support allowed a behavioural change in capture probability (g0) after first capture. Previously uncaught birds had an estimated capture probability of 0.04 (CI: 0.03, 0.07) when at zero distance from the net, while after capture this reduced significantly to 0.005 (CI: 0.002, 0.01).

The density surface modelling suggested an even distribution of birds throughout the reedbed during the breeding season, with the homogeneous, null, model gaining most support (*Table 3.3*). Models with a second and third order terms in the north to south direction gained some support, predicting slightly reduced densities at the reedbed edges (*Figures 3.2, 3.3*).

3.4.2 All individuals over the full year

Over the full year 357 mist-nets were set. The average number of nets opened per month was: 8 at Powgavie, 5.5 at Kingston, 8 at Tay Lodge and 10 at Seaside. 847 birds in total were captured, with 100 individuals captured twice and 8 captured three times. These recaptures are detailed in Appendix 3i. 439 were males, 385 were females while 23 were unknown. Closure tests suggested this population was not closed ($z = -5.52$, $P<0.01$). This may be due to the large influx of juveniles during the breeding season and possibly winter survival. The most supported population model suggested the probability of capture (g0) varied between each sampling occasion (*Table 3.2*). This model suggested a density of 13.47 (11.50, 15.78) birds per hectare. *Figure 3.4* shows the model estimates of g0 for each occasion, and the total trap usage in each occasion. If bias in capture probability was caused by changes in netting effort between occasions, we would expect estimates of g0 to correlate with netting effort, however we found no evidence of this (Pearson's $R = 0.33$,

P=0.28). The most supported density surface models suggested a smooth in the west to east direction (*Table 3.3, Figure 3.2*), with highest densities predicted around Seaside.

Adults during the breeding season

Model	ΔAIC	g0	σ	D (birds per hectare)	N (birds in full study region)
g0 ~ B, σ ~ 1	0	0.042 (0.026, 0.069)	620 (458, 839)	0.59 (0.44 0.77)	134 (101, 176)
g0 ~ T, σ ~ T	18.27	0.0084 (0.0034, 0.021)	313 (199, 495)	4.99 (2.54, 9.84)	1141 (580, 2245)
g0 ~ 1, σ ~ T	18.68	0.0052 (0.0026, 0.010)	889 (541, 1460)	2.67 (1.42, 5.04)	610 (324, 1150)
g0 ~ T, σ ~ 1	23.36	0.0035 (0.0014, 0.0088)	681 (467, 993)	3.55 (1.65, 7.62)	811 (378, 1741)
g0 ~ 1, σ ~ 1	24.52	0.0052 (0.0027, 0.0099)	641 (450, 912)	2.26 (1.26, 4.08)	516 (287, 926)

All individuals throughout the full year

Model	ΔAIC	g0	σ	D (birds per hectare)	N (birds in full study region)
g0 ~ T, σ ~ 1	0	0.0015 (0.0010, 0.0022)	1346 (1148, 1578)	13.47 (11.50, 15.78)	3075 (2625, 3602)
g0 ~ T, σ ~ T	15.94	0.0016 (0.0011, 0.0022)	1150 (688, 1553)	13.12 (11.18, 15.39)	2994 (2551, 3513)
g0 ~ 1, σ ~ T	51.14	0.0019 (0.0015, 0.0024)	1089 (648, 1830)	14.95 (12.55, 17.79)	3411 (2866, 4061)
g0 ~ 1, σ ~ 1	429.22	0.0018 (0.00154, 0.0023)	1520 (1300, 1778)	15.14 (12.81, 17.91)	3457 (2924, 4088)

Table 3.2 – Most supported SECR observation models and associated parameters for the two separate datasets. ΔAIC values represent the difference in AIC values between the given model and the most supported model. Numbers in brackets are 95% confidence intervals for the parameters. Note, due to lack of convergence, the results of the behavioural model (g0 ~ B, σ ~ 1) in the full year dataset are unavailable.

Adults during the breeding season		All birds throughout the full year	
Density surface model	ΔAIC	Density surface model	ΔAIC
Homogeneous (Null) Model	0.00	West to East (3^{rd} Order)	0.00
South to North (2^{nd} order)	4.40	West to East (2^{rd} Order)	1.25
South to North (3^{rd} order)	6.68	Homogeneous (Null) Model	32.32

Table 3.3 – Top three density surface models for the two separate datasets. ΔAIC values represent the difference in AIC between the given model and the most supported model.

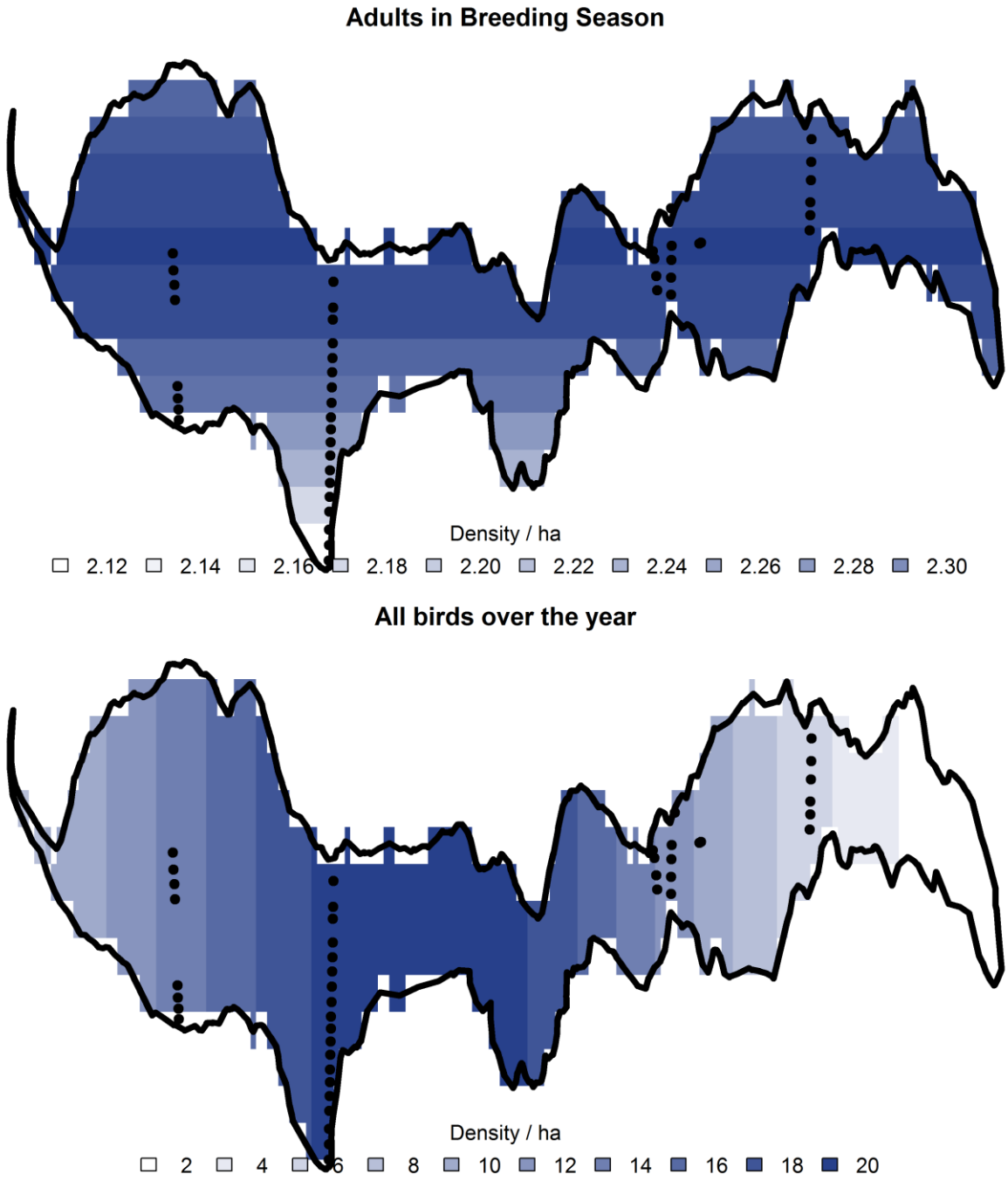


Figure 3.2 – Predicted density of adult Bearded Reedlings from the second most supported density surface when modelling adults only during the breeding season, and the most supported density surface for all birds throughout the full year (see Table 3.2). Dark blue areas represent patches with highest density. Reedbed has been stretched on the Y axis for clarity, with the top edge being the land boundary and the lower edge being the water boundary.

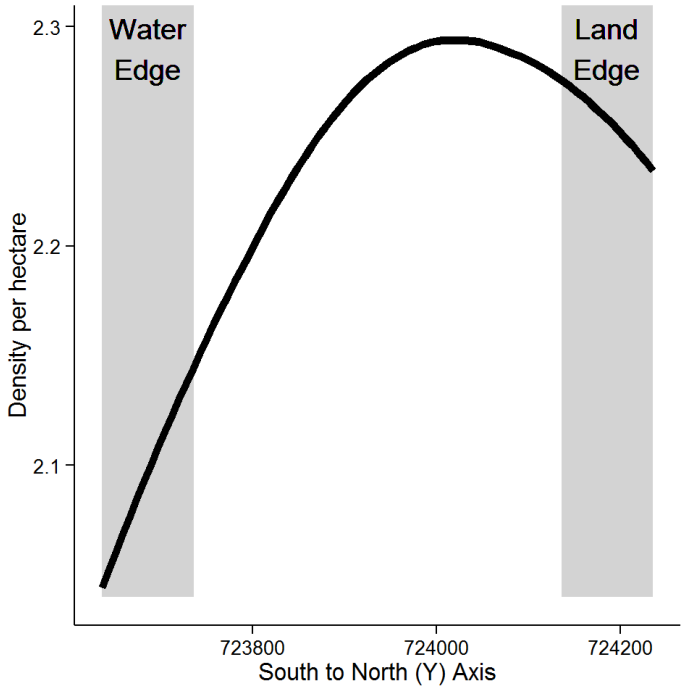


Figure 3.3 – Predicted density from the most supported inhomogeneous density surface, of adult Bearded Reedlings during the breeding season, along the south to north axis. Shaded areas represent the first 100 metres of the reedbed at the land and water edges.

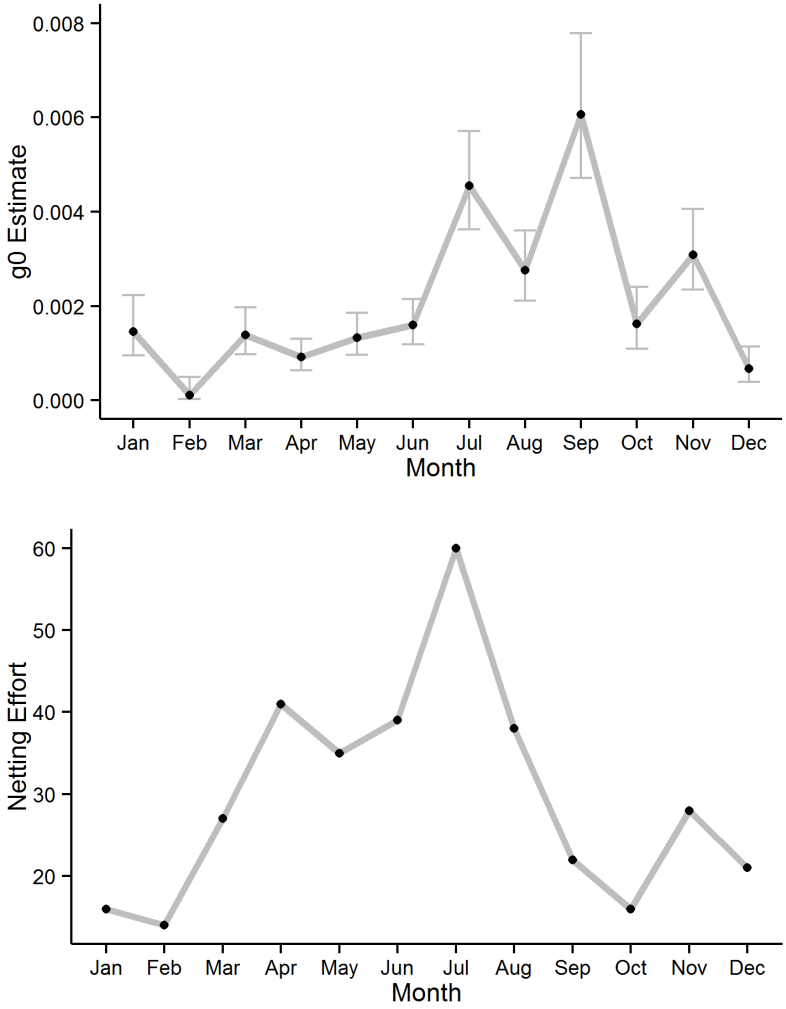


Figure 3.4 – Upper panel: Estimates of the probability of capture (g0) and associated 95% confidence intervals, in each occasion as predicted by the most supported observation model for the full year dataset. Lower panel: Netting effort represented by the total number of nets run in each occasion.

3.5 Discussion

During the breeding season of 2014 we estimated 134 (CI: 101, 176) adult Bearded Reedlings occupying the Tay Reedbeds. These numbers are slightly reduced from the 190 (CI: 148, 271) birds estimated by (Peach 2000) for the 2000 breeding season. However, the overlap in the confidence intervals suggests there has not been an alarming decline in breeding numbers over the last decade. This population remains the only consistent breeding site of these birds in Scotland. For the British Isles as a whole, the rare breeding birds panel offers useful yearly estimates, collating counts during the breeding season from around 60 sites and suggesting an average of 527 breeding pairs for the five years including and previous to 2012 (Holling and RBBP 2012). As these birds are monogamous (Cramp and Perrins 1993, Surmacki *et al.* 2015) and adult sex ratios were equal, our estimates suggest around of 67 pairs occupying the Tay, equating to 12% of the full UK population.

Our analysis of birds occupying the Tay throughout the full year further emphasised the importance of this site for Bearded Reedlings. We estimated 3075 (CI: 2625, 3602) unique individuals on the Tay throughout the year. The vast majority of these birds would be juveniles, which become indistinguishable from adults on completion of their full post juvenile moult at the end of August (Pearson 1975, Svensson 1992). The high investment breeding strategy of the Bearded Reedling may result in occasional productive years (Bibby 1981, 1983, Surmacki and Stępniewski 2007). This species is multi-brooded, having four or more broods between April and August if conditions permit (Bibby 1981, Cramp and Perrins 1993, Surmacki and Stępniewski 2007). Surmacki *et al.* (2003) report average brood sizes of Bearded Reedlings in western Poland as 5.5, while similar sizes have been recorded from samples on the Tay (average 5.6, Chapter 6). Thus, even accounting for potentially high predation rates in reedbeds (Batáry and Báldi 2004, Báldi and Batáry 2005) single pairs can be highly prolific resulting in large influxes of juveniles in years with high nest success. Weather conditions during the breeding season of 2014 were ideal when rearing multiple broods, offering mild conditions after mid-April that continued until August and likely resulting in an exceptionally productive year at this site. Despite this high productivity, the numbers of birds estimated as occupying the Tay Reedbeds throughout the full year is still considerably higher than would be expected from the estimated number of breeding adults. This may have been caused by the lack of closure in the population during the full year period resulting in overestimates of density during this period.

While, overall, these numbers are small in a European context, where a total of 240,000 to 480,000 breeding pairs are estimated (BirdLife International 2014), the Tay Reedbeds may be of international importance in range expansion. This site is on the northern fringe of the species'

range, with only a few Scandinavian populations occurring at higher latitudes. The Tay may therefore act as a northern stronghold for these birds, facilitating dispersive movements. This may be especially important on exceptionally productive years such as 2014. Spitzer (1972) and independently Pearson (1975) suggest that Bearded Reedlings exhibit 'high flying' activity over the reedbeds in early autumn. In low density populations this normally results in birds settling within the same reedbed. However, when population sizes are at their highest, Spitzer (1972) suggests these movements become increasingly excited, resulting in flocks leaving reedbeds and undertaking considerable movements. Indeed, autumn 2014 resulted in the first long-distance recoveries of Bearded Reedlings originating from the Tay, with birds moving up to 40km. While further research into the function of such movements is critical, their potential role in facilitating dispersal may suggest the Tay population has a critical role in site expansion.

To utilise the SECR modelling approach when estimating population sizes, the field methodology involved simple refinement of the ringing protocol already implemented on the Tay. In order to record movements, ringers had to note the exact nets from which each individual was extracted. In most cases this was achievable, with ringers only reporting difficulties when field teams were limited or during the large catches. Nets were placed in clusters at the four most accessible sites with the aim to capture short, within-cluster, movements of birds, and the longer distance, between-cluster movements, occurring during the full year. Despite this, a major difficulty when implementing the SECR analysis was the lack of spatial recaptures. These were especially sparse in the breeding season when only 10 birds were recaptured. While, in this analysis, we were able to augment the models using radio-tracking data, methods with which to integrate telemetry data into the maximum likelihood function are preliminary and in need of further refinement (Efford *et al.* 2015). Additionally, the models can gain most information from telemetry data only when tracked individuals are a subset of those captured in the capture-recapture study (Efford *et al.* 2016). Such data are unlikely to be available in subsequent seasons and could severely impede the use of SECR methods if spatial recaptures remain low. A potential solution could be to undertake a higher effort ringing strategy during occasional breeding seasons, designating additional sites and undertaking more ringing sessions.

However, our modelling process suggested a reason for the low recapture rates could be a learned trap response, with birds avoiding the nets after first capture. This is common in many bird species, with several studies showing reductions in captures of local birds after several days of mist netting activity (Macarthur and Macarthur 1974, Manly 1977, Keyes and Grue 1982). When controlling for this learned response by including an additional parameter in the detection model,

estimates of density decreased by almost 400% in comparison with the null models. If relevant outside of the breeding season this behavioural effect may have caused considerable bias in our analysis of the full year dataset as, due to converge problems, it remained inestimable in this context and untested against other models. However, behavioural models have gained little support in previous, non-spatial analyses of this species with either null or time dependent models being preferred (Peach 2000, Wilson and Peach 2006). The model with most support in the full year analysis was one that allowed capture probability to change between each occasion. As this detectability did not correlate with netting effort, time dependence was not driven by changes in sampling effort. Instead, the time dependent model controlled for the influx of juveniles in the late summer, increasing capture probability to account for the high numbers of independent young.

The density surface models offered interesting insight into the distribution of birds throughout the reedbed. While an inhomogeneous surface gained most support in the breeding season, there was some suggestion that Bearded Reedling abundance was reduced towards reedbed edges. The SECR models estimate the density of animal activity centres, which are a hypothetical point location over which the animal concentrates highest activity (Borchers and Efford 2008, Borchers 2012, Efford and Fewster 2013). In the breeding season activity centres are likely to be around nesting sites. Several studies have shown increased nest predation rates towards the edges of reedbeds (Picman *et al.* 1993, Batáry and Báldi 2004, Batáry *et al.* 2004, Báldi and Batáry 2005, Malzer and Helm 2015). Our tendency to capture birds in the centre of the reedbed potentially reflects the avoidance of this edge effect when birds are positioning their nests. In the full year dataset, density surfaces that allowed flexibility in the west to east direction gained considerably higher support than null models. This suggested sparse abundance around the east of the reedbed, and contrastingly, up to 20 birds per hectare in centre of the study area. This distribution is well supported by field observations. It may additionally reflect the tendency of birds to congregate around dry areas in the winter (Surmacki and Stepniewski 2003, Wilson and Peach 2006), with the models suggesting highest abundance in an old, previously unmanaged, patch of reeds.

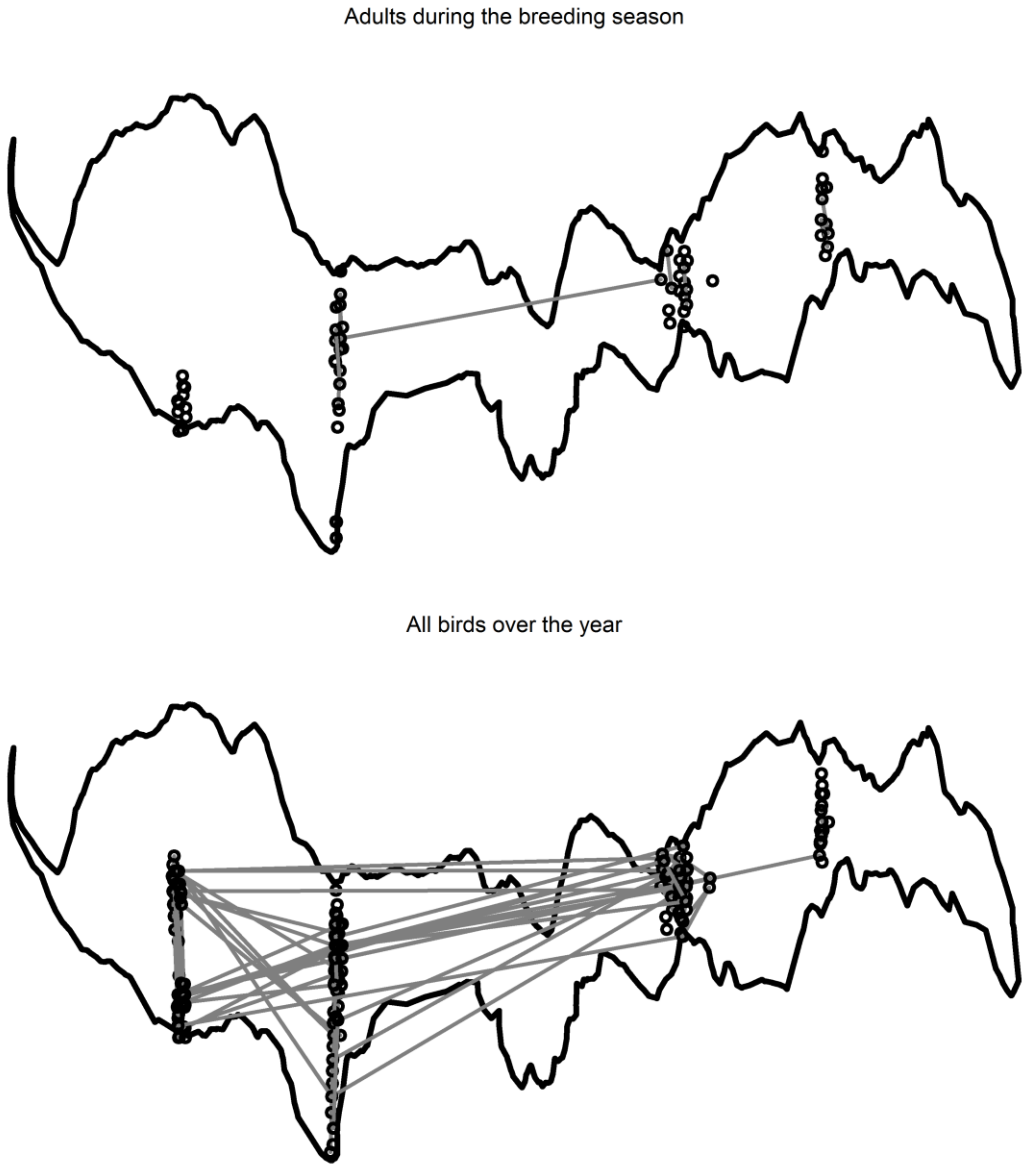
In conclusion, we implemented spatially explicit capture-recapture methods to estimate the population of Bearded Reedlings on the Tay Reedbeds. While spatial recaptures were low, we were able to effectively model the detection process and provide current estimates of the population over an explicitly defined sampling region. The analysis suggested high numbers of Bearded Reedlings occupy the Tay, and that these can increase exceptionally after a productive breeding season. In addition, this modelling approach provided a useful indication to how these birds are distributed throughout the reedbeds. We recommend the continuation of this protocol only if the numbers of

spatial recaptures can be increased through the occasional year of high effort mist netting and ringing surveys. This would allow a consistent approach, unbiased by incomplete coverage, for the long term monitoring of this elusive, specialist species.

3.6 Acknowledgments

We thank the Carnegie Trust for funding this research. We would also like to thank all of the members of the Tay Ringing Group who assisted with the mist-netting and ringing, especially, Mike Nicoll, Steve Moyes, Bruce Lynch, Derek Robertson, Geoff Flogdell, Les Hatton and Shirley Millar. Further thanks to Shirley Millar for patience and guidance when processing the ringing data. We thank David Borchers and Murray Efford for thoughts, comments and assistance with the analysis. Finally, we thank RSPB Scotland for maintaining the mist netting rides and providing valuable insight throughout the study.

3.7 Appendix 3i – *Recaptures of Bearded Reedlings between nets on the Tay Reedbeds, Scotland. Open circles are individual captures with a degree of radial jitter to avoid over-plotting. Solid lines represent 'spatial recaptures', recaptures of birds at different nets on separate occasions. Top panel shows few spatial recaptures of adults during the breeding season, with most occurring within clusters of nets, and only one movement between clusters. Lower panel shows many spatial recaptures during the full year dataset.*



Chapter Four

The habitat selection of a specialist reed Passerine in a mosaic managed reedbed.

Iain Malzer, Stewart White, Barbara Helm

4.1 Abstract

In studying animal space use we can infer important resources and habitats, information that can be directly incorporated into conservation management. Reedbeds are a rare wetland habitat which is often extensively managed for commercial or conservation motives. Mosaic reedbed management, which involves small scale winter cutting, may provide an effective compromise between these motives. As several specialist birds rely on reedbeds, understanding the effects of such management on space use and resource selection is imperative. We inform reedbed management on the consequences of mosaic reed cutting for the space use and resource selection of a specialist reedbed passerine, the Bearded Reedling, *Panurus biarmicus*. This species is strongly associated with reedbed habitats, changing its diet seasonally, from insects in the summer, to reed seed in the winter, allowing it to remain in local reedbeds throughout the year. We conducted a long term point count survey of Bearded Reedlings on a mosaic managed reedbed in Scotland to indicate how distribution at the population level changed in relation to management. We then radio tracked individuals during two breeding seasons and one autumnal season, establishing how birds select specific reed categories created by management from the full study site and from within their home range during foraging trips. Our results suggest that, during the breeding season, mosaic management did not affect the distribution of birds throughout the reedbed. However, it may alter fine-scale foraging decisions, with birds in managed areas selecting young and cut reed during foraging trips. In the winter and autumn, birds consistently selected old reed, which had a high leaf litter. This study provides insight into dynamic space use of a highly specialised reedbed passerine which can be directly incorporated into conservation management strategies for this species and reedbeds generally.

"He learned to communicate with birds and discovered their conversation was fantastically boring. It was all to do with windspeed, wingspans, power-to-weight ratios and a fair bit about berries."

Douglas Adams, So Long and Thanks for all the Fish

4.2 Introduction

By understanding how animals distribute themselves throughout space, inferences can be made about important resources and habitats. This is often conducted by observing the use of certain habitat features in relation to their availability (i.e. resouce selection; Johnson 1980, Thomas and Taylor 1990, 2006, Manly *et al.* 2002). Resource selection can be explored over a hierarchy of selection orders, ranging from population level spatial scales, to the individual (Thomas and Taylor 1990, Manly *et al.* 2002, Battin and Lawler 2006). For example a population may form aggregations in a specific important habitat disproportionally to the availability of that habitat in the wider environment (Johnson 1980, Marcum and Loftsgaarden 1980, Morris 1987). Similarly, individual home ranges may include more of a specific habitat than would be expected from its availability. Finally, individuals may show selection decisions within their home ranges during distinct ecological activities. Studies concerning these orders are classified as design 1, 2, and 3 studies respectively (Johnson and Temple 1990, Thomas and Taylor 1990, Manly *et al.* 2002).

Resource selection studies at appropriately defined selection orders are of clear use when managing wildlife. Population order designs (design 1) allow identification of key habitats from counts of unmarked individuals (Stinnett and Klebenow 1986, Corriale and Herrera 2014). Advances in biotelemetry methods have allowed the collection of individual habitat selection data (Kays *et al.* 2015), which can inform management of temporal or individual variation in resource selection (design 2)(Roy and Dorrance 1985, Sawyaer *et al.* 2001, Chudzińska *et al.* 2015). Design 3 studies have demonstrated individual habitat selection within home ranges, and allowed identification of specific selection during distinct periods such as nesting, foraging or roosting (Aubry and Raley 2002, Arroyo *et al.* 2009, Palatitz *et al.* 2011, Dwyer *et al.* 2013). Information regarding animal resource selection can therefore contribute key evidence into the often contentious debates surrounding appropriate ways to manage the environment.

One such debate surrounds the management of reedbed habitats. Common reed, *Phragmites australis,* is a tall perennial grass that forms large single species stands along the interface between terrestrial and aquatic environments (Stance 2010). Reedbeds are an intermediate stage of vegetative succession, producing a rapid accumulation of leaf litter (Cowie *et al.* 1992) which, without regular removal, can allow a foothold for pioneer scrub species (Hawke and Jose 1996, Stance 2010). The naturally temporal nature of reedbeds and dramatic effects of 'reed dieback' (Ostendorp 1989, Graveland 1998, Gigante *et al.* 2014), have contributed to an alarming decline in this habitat throughout Europe, which is exacerbated by extensive drainage schemes preventing new reedbed sites becoming established (Bibby and Lunn 1982, Everett 1989). This loss

of habitat presents a major threat for several specialist reedbed species (Cramp and Perrins 1993, Graveland 1998, Poulin and Lefebvre 2002). It is therefore of critical conservation importance that appropriate management strategies are established for reedbeds and their associated biodiversity.

Majorly, reedbeds are managed by altering water levels or cutting the reed (Hawke and Jose 1996). Maintenance of water levels above the soil surface and winter reed cutting can assist in the removal of leaf litter, processes vital when preserving the dominance of reed. Reed management may have commercial motives, being cut for use as thatch (Poulin and Lefebvre 2002). In this case, old patches of reed are initially cleared to stimulate new reed growth. Patches of this new, young, reed can then be cut in subsequent winters either, every year (single wale) or on a more rotational basis (double wale) (Hawke and Jose 1996). In purely commercially harvested reedbeds, large areas of the stand are clear cut to maximise yield. At a large scale this can be detrimental to the habitat and associated wildlife as there is no reed available after the cutting dates until it has grown back by around June. This method can be especially detrimental to early nesting species which require the reed from March. Conversely, reed cutting may be undertaken for conservation, in which case, smaller patches or blocks of reed are removed during the winter, leaving a mosaic of old and cut reed. Cutting can increase the vigour of the reed, stimulating new growth to outcompete pioneer species and consequentially preserving the long term integrity of the stand. The resulting mosaic of reed ages produced by conservation driven reed cutting also increases structural heterogeneity throughout the stand, with the aim to benefit biodiversity (Hawke and Jose 1996, Beemster *et al.* 2010, Trnka *et al.* 2014).

The debate surrounding which of these management regimes offers a reasonable compromise between commercial and conservation motives, stems from wide variation in the recorded effects of reed cutting. Valkama *et al.* (2008) performed a meta-analysis of 21 studies conducted in reedbed sites and show reed cutting caused considerable changes to the structure of reed, with cut stems growing back to a lower height but at higher density. They also demonstrated a reduction in invertebrate abundance and diversity, but this effect was both time dependent and variable between orders and families. While this analysis suggested reed cutting has, generally, negative consequences for wildlife, recent studies suggest mosaic reed cutting could mitigate these impacts. Trnka *et al.* (2014) show the retention of old reed during mosaic management allowed invertebrates to rapidly reoccupy neighbouring cut sites after regrowth. Further, Beemster *et al.* (2010) show that a mosaic of old and younger, recently grazed, reed can provide reed passerines with nesting and foraging sites respectively.

In driving these structural changes in the reed, reedbed management may influence resource distribution and ultimately alter the space use of animals. Reed specialist passerines offer a useful system with which to investigate the effects of reedbed management on animal space use. These species are mobile, and thus more freely able to choose from locally available resources or habitats than other species. Additionally, the fitness of several reed passerines is known to be influenced by the quality and structure of the reedbed (Graveland 1998, Wilson and Peach 2006, Darolová *et al.* 2014). Thus, progressive reedbed management, in which conservation and commercial motives are satisfied, will benefit from research into the spatial associations of reed passerines with various management regimes. Consequentially, several studies have monitored the effects of reed cutting on bird abundance at the population level (Poulin *et al.* 2000, 2002, Barbraud and Mathevet 2002, Trnka and Prokop 2006, Beemster *et al.* 2010). These studies show little consensus due to a wide variation in study species and site, with the most comprehensive a meta-analysis (Valkama *et al.* 2008) eluding to a general reduction in bird abundance in cut reed patches. In order to better inform reed management strategies, the causes of this variation requires further study. Importantly, as previous studies concern population level space use, information concerning the fine-scale, individual level, variation in the space use of reed specialist passerines may be especially valuable. Such information can be gained in design 2 and 3 resource selection studies. Design 2 analyses can provide information of general patterns of habitat selection at the individual, while design 3 analyses can highlight variation in habitat analysis between individuals. These may better highlight the most important structural changes to the reed caused by management, emphasise important individual variation in space use and ultimately assist in unravelling the mechanisms driving space use in reedbeds.

We observe the space use of a true reedbed passerine, the Bearded Reedling, at different resource selection orders to guide reedbed management on the consequences of reed cutting for this species. The Bearded Reedling is strongly associated with reedbeds, being rarely located outwith these habitats. Part of the population remains in local reedbed sites the full year (see chapter 8), meaning that the implications of management will only be fully understood if different seasonal perspectives are considered. In autumn, rather than engaging in obligatory migration with many other reed specialists (Leisler 2011), these birds undertake considerable changes in gut morphology (Spitzer 1972) which allow them to remain locally by switching diet from invertebrates in the summer, to reed seeds in the winter (Bibby 1981, Wilson 2014). The dependence of Bearded Reedlings on rare reedbed habitat, and the tendency for populations to undergo wide fluctuations (Korpimäki 1986, Wilson and Peach 2006), are a strong motivation to better establish conservation management strategies for this species, to which studies of fine-scale space use could directly

contribute. Previous studies have demonstrated non-homogeneous space use of this species throughout reed stands at the population level (design 1), with higher nest abundance in old reed stands (Hoi 1997) and directed foraging trips in wet or recently grazed reed (Bibby 1981, Hoi 1989, Beemster *et al.* 2010). However, no previous study has considered fine-scale, individual level, habitat selection of Bearded Reedlings and how this is influenced by mosaic reedbed management.

We first monitor the distribution, at a population level, of Bearded Reedlings throughout a mosaic managed reedbed over the course of a two-year study. We do this by conducting a consistent point transect survey each month, allowing an estimate of density between cut and uncut patches of the reedbed during key seasonal phases. These data allow insight into how the distribution of the general population changes over the year and in relation to reedbed management. We then present design 2 and 3 habitat selection data, acquiring fine-scale distribution data from a sample of radio tagged individuals during the breeding and autumnal periods. We quantify these data by observing the tendency of birds to use patches of reed that differ due to management and location (referred to as "reed categories", see Methods), in relation to their availability. The design 2 analyses examine the overall selection throughout the reedbed during these seasonal phases. A design 3 analysis is then implemented during the breeding season to identify the selectivity of foraging resources by an individual within its local home range. Finally, we investigate the potential mechanisms driving the exposed distribution and habitat selection by quantifying changes in the structure of the habitat, and prey abundance between reed categories throughout the year.

4.3 Methods and Materials

4.3.1 Study Site

The study was undertaken from April 2013 to May 2015 in Tay Reedbeds, on the northern side of the Tay Estuary, Scotland (56°23.00'N, -3°10.00'W). At 4.1km^2 these are the largest continuous reedbeds in the British Isles, consisting of uninterrupted stands of Common Reed, *Phragmites australis*. These reedbeds were colonised by Bearded Reedlings in around 1990, and are positioned at the northernmost edge of the species' distribution in the United Kingdom. We focused on a 2.2km^2 area of the reedbed between Port Allen (56° 22.70'N, -3° 12.432'W) and Kingston (56° 25.89'N, 3° 7.31'W) which includes the historical strongholds of Bearded Reedlings on the Tay, with around 100 breeding pairs (Peach 2000, also see Chapter 3), and adequate areas of different management regimes for comparison. Since 2005 reedbed management has been undertaken to preserve the long term integrity of the reedbed and provide structural heterogeneity in the reed for breeding birds. Under this management plan, single wale mosaic reed cutting was conducted on no more than 20% of reedbed area between November and February each year. The cutting pattern over the duration of the study (2013-2015) allowed the study area to be split into two major regions: an intensively managed region, 0.84km^2 in area, in the east of the study area and a largely unmanaged region of 1.36km^2 in the west (*Figure 4.1*). We use the terms "managed" and "unmanaged" to refer to these regions throughout.

Within the managed region, reed cutting over the duration of the study was conducted on exactly the same patches of reed each winter, creating the same mosaic of reed heterogeneity each year of the study (*Figure 4.1*). Cut patches were on average 0.003 km^2 in area, equating to 19% of the managed region. In the years prior to the study, slightly different patches were cut, meaning that the mosaic in the managed region was made up of reed cut the previous winter, reed which had not been cut for 1-5 years, and previously uncut reed. The unmanaged region was left mostly uncut over the study, except three patches cut only during the winter of 2013, which made up 3% of its area (*Figure 4.1*). This meant that, while old, uncut, reed made up the vast majority of the unmanaged region, it also included a small section of reed that changed from cut reed in 2013 to young reed in 2014 and 2015.

Additionally, in order to capture potential ecological changes throughout the year, datasets were split into a seasonal calendar relevant to the Bearded Reedling. Each month of the study was pooled into either the breeding period, autumnal period, or wintering period (*Table 4.1*). Grouping was based on the wider ecological patterns of this species (Pearson 1975, Bibby 1981, Cramp and

Perrins 1993), being slightly altered based on local knowledge of birds on the Tay. For example, Tay birds begin breeding in April, rather than March as reported for birds elsewhere in the British Isles (Bibby 1983, Wilson 2005).

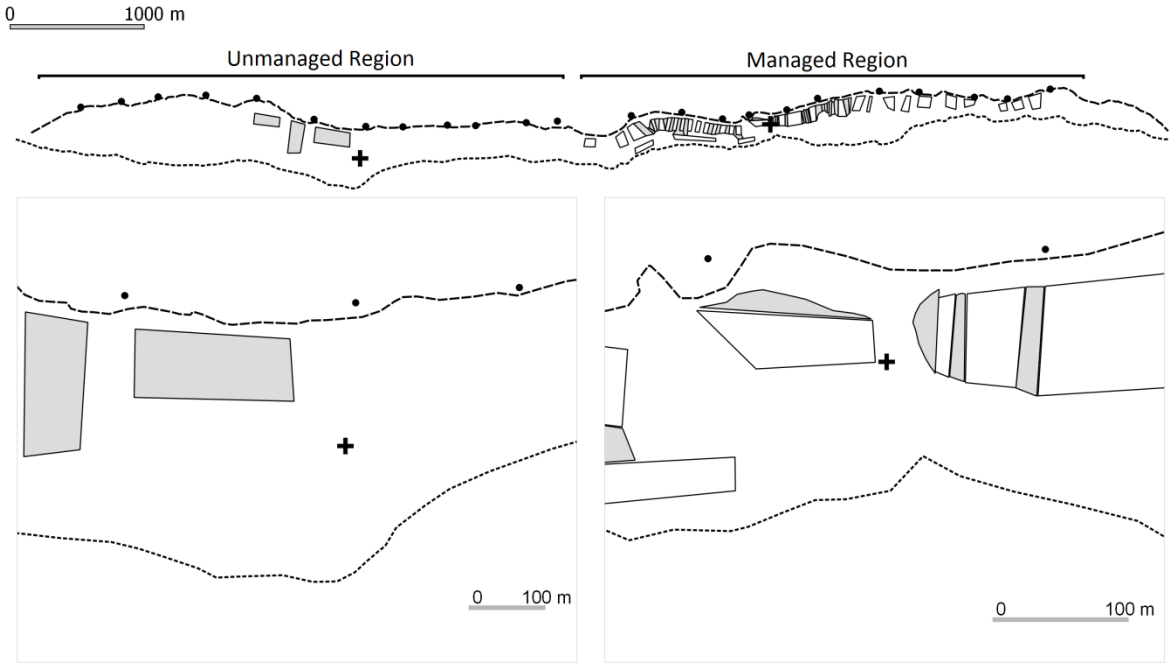


Figure 4.1 – Study area in the Tay Reedbeds, Scotland, split between managed and unmanaged regions. Maps below show small sections within each region at a larger scale. Solid points on bank represent the point transect. Crosses represent transmitter attachment sites. White squares depict reed cut the previous winter, grey squares represent young reed, remaining areas are old, uncut reed. Dashed line is the land edge, while the dotted line is the river edge.

Year	Seasonal Phase	Months Included	No. of Bank Surveys	No. individuals Radio Tagged.
2013	Breeding Season	April – July	4	0
	Autumn	August – October	3	20
	Winter	November - December	4	0
2014		January – March		
	Breeding Season	April – July	4	22
	Autumn	September – October	2	0
	Winter	November - December	5	0
2015		January – March		
	Breeding Season	April – May	2	11

Table 4.1 – Data collection periods placed in relevant seasonal phases of the Bearded Reedling. Note, the number of surveys is lower than expected as no data are available for December 2013 or October 2014.

4.3.2 Population Level Distribution (Design 1)

Bearded Reedlings were monitored each month at the population level using a point count transect. This allowed comparisons between densities of birds occupying cut and uncut areas throughout the year. The transect survey consisted of 23 vantage points located on the bank of the reedbed between 300 – 500m apart, in areas that offered unimpeded views (*Figure 4.1*). At each point, only the first 100m of the reedbed could be adequately surveyed. Edge effects (Báldi and Kisbenedek 1999, Moskát and Báldi 1999, Trnka and Prokop 2006) and conducting surveys along linear features (Marques *et al.* 2010) can bias estimates of abundance if extrapolated. Thus, the survey was not designed to draw conclusions about the overall abundance of birds in the full reedbed, but rather allow relative comparisons of density over time and between cut and uncut patches.

On arrival at a point two minutes of settling time were designated after which five minutes of observations were conducted. The number of individual Bearded Reedlings were noted, as was the distance of each observation into intervals of 0-10m, 10-20m, 20-30m, 30-40m, 40-60m, 60-80m, 80-100m and beyond 100m. Distance estimation was aided by the edges of cut areas, pools or trees which were visible from the point and of known location in the reeds. When birds occurred in

groups the number of individuals within each group was estimated by recording the highest number of the birds seen at the same time. The presence of coloured rings and sexual dimorphism assisted when estimating group sizes.

4.3.3 Radio Tracking (Designs 2 and 3)

A total of 32 Bearded Reedlings were radio tagged during the early breeding season, 21 in 2014 and 11 in 2015. 20 birds were tagged in September 2013 (*Table 4.1*). Initial capture and attachment of the transmitters occurred in both the managed and unmanaged regions, with the aim to tag equal numbers of birds in both regions (*Figure 4.1*). In the breeding seasons, attachment was timed with the first appearance of breeding traits, such as the brood patch or conspicuous cloacal protuberance, in birds monitored during ringing sessions. In both years, birds from the managed and unmanaged regions showed synchrony in the appearance of breeding traits, allowing tags to be deployed over the same period. In the autumnal period, birds were tagged in mid-September, which is when they are expected to begin digesting reed seed (Wilson 2014). Radio transmitters (0.4g PIP3 single celled tags; maximal dimensions 7mm x 7mm x 4mm; battery type Ag337; Biotrack, Dorset, UK) were first sewn onto a square of cotton cloth (surface area $1cm^2$). A patch of feathers of similar size on the central upper back of the bird was then trimmed before the cloth was glued to this area using latex based eyelash glue. The tags were 0.025% of the mean weight of all the birds tagged over the study (15.5g) and never exceeded 0.03%. Using this method, tags were expected to remain attached for between 3 and 4 weeks, thus, in both breeding seasons, tags were active from mid-April to mid-May. In autumn 2013, tags were active from mid-September to mid-October.

The birds were then tracked by triangulating the position of the radio signal from the bank of the reedbed using two Biotrack SRX600 VHF radio receivers with flexible Yagi antennas. Simultaneous bearings were collected by two field researchers standing between 50 and 100m apart. Triangulation was then conducted using QGIS software (QGIS Development Team 2012). Preliminary information was collected on the accuracy of the locations estimated from triangulation by leaving transmitters in known positions throughout the reedbed and comparing these with the estimates. 15 trials suggested the transmitters were accurate to with 12.5m when three bearings were taken. In the breeding season, bearings were taken every 15 minutes for a period of 4 hours, after which the researchers would move to a different individual and conduct the same protocol. In September, birds were more spread out and tended to move considerable distances. During this period, locations were collected twice a day for each individual. Triangulation periods could be conducted during any daylight hour. Locations were also collected from direct sightings of tagged individuals.

In the breeding season, every day that an individual was tracked it was assigned to a specific 'breeding phase' either: non-breeding, incubating, feeding chicks, or feeding fledged chicks. Non-breeding phases could include the locations taken prior to nesting and the time between nesting attempts. Birds were considered incubating if, either, the nest was located and confirmed this, or birds showed clearly stationary periods interspersed with bouts of activity. Stationary periods were readily identifiable using the tracking equipment. The receivers were sensitive to movement and changes in the physical orientation of the bird towards the receiver, so that stationary periods indicated rest or incubation. Birds were normally conspicuous during the chick provisioning phase, carrying food back to the nest area. At this stage, the location of the nest, if not directly accessible, could be accurately estimated to within 20m.

Foraging trips were considered as all locations that occurred over 20m away from the nest during incubation and chick provisioning. To minimise locations collected when the individual was actively moving between the nest and foraging area, triangulations were conducted only when the signal was picked up from a consistent direction. Additionally, to avoid the duplication of points collected during the same foraging trip, only one point every 30 minutes was considered when birds were incubating, while this threshold was reduced to 15 minutes when birds were provisioning young, as during this phase, distinct feeding trips were frequent and more easily distinguishable.

4.3.4 Habitat data and invertebrate analysis

In order to establish differences in reed structure between the habitat categories, we measured characteristics of the reed within each category throughout the year. A minimum of 10 points were visited within each reed category bi-monthly over the duration of the full study period. *Table 4.2* details the methods used for habitat measurements. Measurements of cut reed were conducted after reed had grown back and reached maturity. The points visited were randomly generated, but constrained to areas of the reed that were accessible. We also explored differences in insect abundance between the habitat categories. Between May and June, 2014, we placed 4 bowl traps at random locations within each category. These consisted of yellow bowls, 10cm in diameter, attached to the top of poles at 1m from the ground. We filled each bowl with 100ml of water, ethanol and a measure of detergent to break the water surface. Bowl traps were left out for 5 days after which all invertebrates were removed and stored in 70% ethanol (Trnka et al, 2015). Those over 2mm in size were then counted and identified to order in the laboratory.

Reed Characteristic	**Methodology**
Height (cm)	Height from the ground to the top of the seed panicle measured to the nearest cm using a tape measure. Average of 5 stems per point.
Density (stems)	Number of stems touching a 1m long stick inserted at a height of 1m off of the ground. Average of 3 measurements per point.
Diameter (mm)	Diameter of stem at 1m off of the ground measured using callipers. Average of 3 stems per point.
Seed Index	The density of stems at the point multiplied by the average length of 5 randomly selected seed panicles, multiplied again by the proportion of 5 randomly selected stems that still retained seed panicles.
Stagger rating (1-5)	The degree of compaction or flattening of reed measured by eye on a scale of 1-5 with 1 being straight, erect reed and 5 being flattened, bent reed.
Leaf Litter Depth (cm)	The depth from the surface of the litter to the ground below measured to the nearest 5cm using a tape measure. Average of 3 measurements per point.
Water Cover %	The percentage of ground submerged underwater estimated using a 0.5x0.5m quadrat. Average of 3 measurements per point.

Table 4.2 – Habitat variables collected, units and methodology used

4.3.5 Statistical Analysis

To estimate relative density from the point count data a conventional distance analysis approach, following Buckland et al (2001), was undertaken in DISTANCE 6.2 (Thomas *et al.* 2010). When fitting detection functions chi-squared tests and observing the model fit over a histogram of detection distances suggested that data should be truncated at 80m. An appropriate shape for the detection function was then estimated by exploring various combinations of key functions (such as half-normal, hazard rate and uniform) and adjustment terms that specified the degree of flexibility in the curve. The fit of the detection function was assessed visually and using chi-squared and AIC methods. Each observation was considered as cluster of individuals of known size and distance from the point, rather than as single individuals. This meant the need to estimate cluster size at zero distance from the point (Buckland *et al.* 2001). To achieve this, we used a regression of log cluster size over distance when the regression was significant to an alpha level of 0.10. When the regression was not significant the mean cluster size in the sample was used.

Each point count was assigned as sampling either "cut" or "uncut" reed during any given survey. Points were considered cut if they were within 100m of a block cut in the previous (or current) winter. Detection functions and density estimates were estimated for the three distinct temporal periods, for each year independently (*Table 4.1*). For each seasonal period, models were post stratified on whether a point was sampling 'cut' or 'uncut' habitat to test whether the presence of cut patches affected density. The relevance of these stratifications was tested against null models using AIC methods.

For the radio tracking data we used R version 3.1.1 (R Development Core Team 2011) package adehabitatHR (Calenge 2011a) to calculate 95% minimum convex polygons (MCPs) for each individual as an estimate of home range size. These sizes were compared between seasons, sexes and regions using T-Tests. Habitat selection was then investigated using Manly selectivity ratios at both design 2 and 3 orders in R package adehabitatHS (Calenge 2011b). For this analysis we categorised all reed in each region into five mutually exclusive groups. These were 'old' reed, which included all areas that had not been managed for over five years. 'Young' reed for areas that had not been cut for between 1-5 growing seasons. Further subdivision of this category was avoided as there were too few areas in each specific age class for comparison. 'Cut' reed was used for areas that had been cut in the proceeding winter. 'Land edge' referred to reed within 20m from the land edge, and 'water edge' for reed within 20m from the water edge. These categorisations were based on evidence that reed cutting and gradients towards the edges of reedbeds can consistently alter the structure of reed growth (Coops *et al.* 1996, Valkama *et al.* 2008). These categories are also directly translatable into management.

In the design 2 analysis we compared the number of locations of each individual that occurred within the habitat categories, to the availability of these categories within the overall study area. The overall study area was defined as the full reedbed and no areas outwith this. This was undertaken individually for the autumnal and breeding season samples. As sample sizes for the 2015 breeding season were low, with only four birds in each region (see *Table 4.2* in results), we pooled the breeding season data from both years. This was justified as the consistent cutting regime meant that the same reed categories were available in the same locations and quantities between each year. In the design 3 analysis we compared the number of foraging trips which occurred in each habitat category, to the availability of these categories within an individual's home range. The availability of the different reed categories within a home range was calculated by constructing a 100% minimum convex polygon (MCP) for all locations collected during the breeding season for the given individual. We added a buffer onto the MCP of half the average distance of the individual's

foraging trips, to reduce the linearity of the MCP and prevent the omission of areas that were clearly accessible and available, but just unused. We undertake no selection analysis of nesting sites as nests were invariably positioned within the 'old' reed category (see chapter 6).

At selection order 2 and 3 we calculated Manly selectivity ratios of habitat selection for each individual, and the global mean of the selection ratios. We tested whether selection was significant using White and Garrott's (1990) chi-squared test, which consists of the sum of the chi-squared values for each individual, and offers a global measure of significance in habitat selection (Manly *et al.* 2002, Calenge and Dufour 2006). We also performed a chi-squared test on the habitat usage table to assess whether the tendencies of selection differed between individuals. Individual variation was further investigated using the eigenvalues of selection ratios (Calenge and Dufour 2006). This approach involves combining White and Garrott's (1990) chi-squared, Manly selectivity measures, and a factorial analysis to emphasise individual differences between habitat use and availability on the first factorial plain (conducted using R package adehabitatHS; Calenge 2011b). The results of the eigenanalysis were then graphically interpreted to identify groups of individuals that showed similar patterns of habitat selection.

We tested for differences in the reed attributes between the five habitat categories using linear models with the given reed attribute (*Table 4.2*) as the response variable and the reed category as a five level categorical predictor. We also added the season in which the measurement was taken as an additional three level factor in the models. In cases where data were not normally distributed we used an appropriate transformation prior to modelling. We used T-tests to verify that the structure of reed within each habitat category was consistent between the managed and unmanaged regions. We used one way ANOVAs to investigate differences in total arthropod abundance between each habitat category. Additionally, as previous studies suggest Chironomids are a key component of the diet of the Bearded Reedling (Bibby 1981, Beemster *et al.* 2010), we specifically investigated differences in the abundance of Nematocera. Chironomids were not directly investigated as invertebrate identification was only to the level of order.

4.4 Results

4.4.1 Population Level Distribution (Design 1)

A total of 552 point counts were undertaken, 256 occurred in points overlooking cut reed, 296 overlooking uncut areas. We observed 226 clusters, and a total of 350 individual birds. Mean cluster size was 1.54 individuals. 2013 saw 14.9 birds per transect, 2014 saw 15.6 and 2015 saw 12.2. A half-normal curve, with a cosine series expansion provided sufficient modelling of the detection function. The distance analysis suggested models that included stratification between cut and uncut reed were more supported (> 2 ΔAIC units) than null models only in the breeding season of 2013 (higher in cut), and both winter phases studied (higher in uncut areas; *Figure 4.2*).

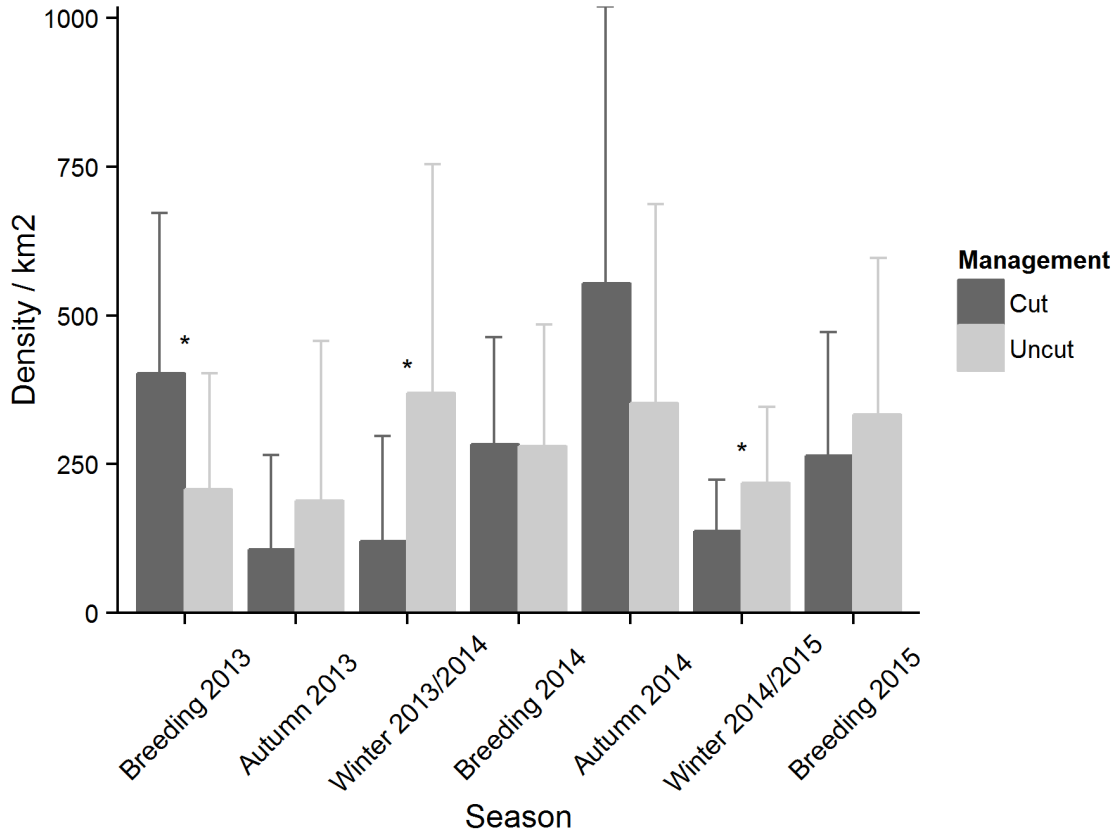


*Figure 4.2 – Density of Bearded Reedlings on the Tay Reedbeds estimated using a conventional distance analysis approach during key seasonal phases. Density is shown for cut and uncut reed, * highlight seasons in which models with management stratification are 2 or more AIC units more supported than null models.*

4.4.2 Radio Tracking

A total of 42 (*80%*) of the radio tagged Bearded Reedlings provided more than 15 relocations and are considered in the further analysis (*Table 4.3*). The average number of relocations per bird was similar for both breeding seasons (2014: 71.8, min: 19, max: 105; 2015: 73.1, min: 50, max: 96), and due to sampling protocol, lower in the autumn 2013 visit (20.3, min: 15, max: 29). Birds tracked in autumn had larger 95% MCPs than those in the breeding season (T-Test, autumn: 0.586 km^2 ± 0.085 SE; breeding: 0.063 km^2 ± 0.006 SE; $t_{17} = 6.11$; $P < 0.001$). There were no differences in 95% MCP area between sexes (T_{13}=0.16; P=0.87*)* or regions where the transmitter was first attached ($T_{4.6}$=-1.18; P=0.29) in autumn*.* In the breeding season, sexes were similar (T_{13}=-0.41; P=0.68*)*, but birds first captured in the managed region had significantly smaller 95% MCPs (T-Test, Managed: 0.039 km^2 ± 0.006 SE; Unmanaged: 0.078 km^2 ± 0.007 SE; $T_{22} = -3.9$; $P < 0.001$).

	Managed		**Unmanaged**	
	Males	Female	Male	Female
Autumn 2013	1	3	7	7
Breeding 2014	4	2	5	5
Breeding 2015	2	2	3	1

Table 4.3 – Sample sizes of radio-tracked birds with > 15 relocations during each seasonal phase.

4.4.3 Habitat Selection Design 2

Bearded Reedlings showed significant habitat selection in September ($\chi2 = 354.18$, df = 72, $p < 0.001$), selecting old reed more than the other habitats (*Table 4.4*). In this season individuals were similar to each other in their selection of the habitat ($\chi2 = 50.7$, df = 68, $p < 0.94$). This was confirmed by the eigenanalysis of the selection ratios, which suggested a single factor explained 97% of the variability in individual selection. In the breeding season habitat selection was significant ($\chi2 = 1958.78$, df = 92, $p < 0.001$) with birds selecting old, young and cut reed over reed at the edges (*Table 4.4).* Selection, however, varied between individuals ($\chi2 = 792.87$, df = 92, $p < 0.001$). The eigenanalysis of the selection ratios suggested two distinct groups which could be attributed to the

separate regions of first capture (*Figure 4.3)*. These two axes explained 83% of the variation (first axis 55%, second axis 28%). Edges were avoided in all cases.

	Breeding Season			**Autumn**		
Habitat	% Avail	% Use	Selection Ratio (SE)	% Avail	% Use	Selection Ratio (SE)
Old	40	65	1.62 (0.10)	40	82	2.06 (0.04)
Young	5	14	2.78 (0.52)	5	1	0.22 (0.14)
Cut	7	10	1.48 (0.45)	7	1	0.06 (0.04)
Land Edge	16	4	0.24 (0.05)	16	2	0.14 (0.05)
Water Edge	32	7	0.22 (0.04)	32	14	0.44 (0.05)

Table 4.4 – Type 2 habitat selection of Bearded Reedlings during the 2014 and 2015 breeding seasons and the 2013 autumn period.

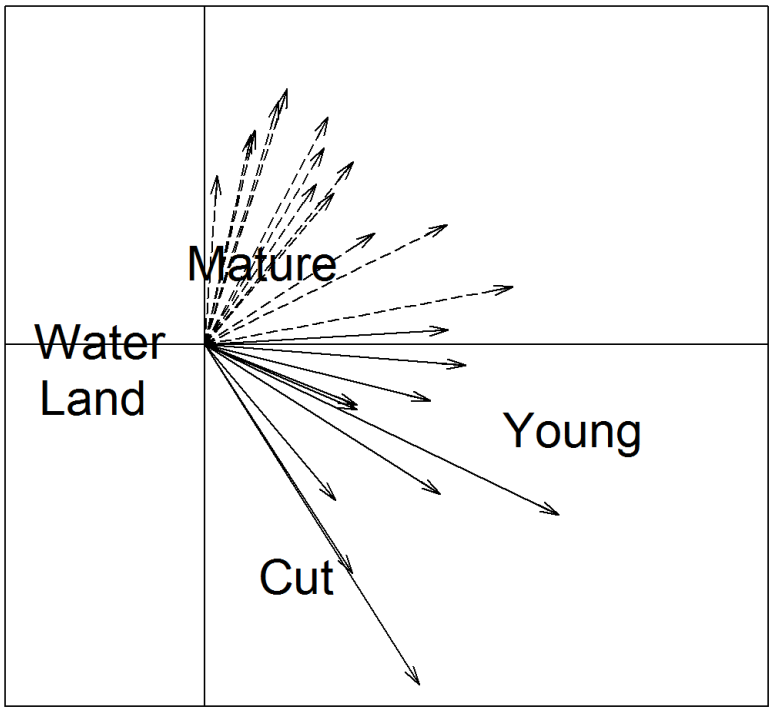


Figure 4.3 – Eigenanalysis of selection ratios of Bearded Reedlings for desgin 2 habitat selection during the breeding season. Labels detail the habitat loadings on the first 2 factorial axes. The arrows are the scores of the individuals on the first factorial plane. The solid arrows represent individuals first captured in the managed region, dashed arrows represent individuals first captured in the unmanaged region.

4.4.4 Habitat Selection, Design 3

100% of the nests were located in old reed. We recorded 1327 foraging trip locations. 601 of these occurred in the managed region, 726 in the unmanaged region. Foraging trips were on average 116.4m (± 2.02 SE) which remained constant between years (2014: 121.4m ± 7.0 SE; 2015: 133.4m ± 11.0 SE t_{13}=0.61, P=0.55). In the managed region foraging trips were significantly shorter in distance (Managed: 97.0m ± 6.7 SE; Unmanaged: 134.2m ± 6.0 SE; T_{20}=-4.07, P<0.001). Distances of foraging trips were similar between sexes (females: 118.9 ± 8.2, males: 118.5 ± 8.7, T_{22}=0.02, P=0.98). As the design 2 analysis suggested habitat selection was dependent on the region of first capture, we constructed design 3 selection ratios for birds first caught in managed and unmanaged regions separately. There was significant habitat selection during foraging trips in the unmanaged region ($\chi 2$ = 70.64, df = 32, p < 0.001) and managed region ($\chi 2$ = 126.18, df = 38, p < 0.001). Young reed was consistently selected for in the managed regions, while birds foraged more in old reed in the unmanaged regions (*Figure 4.4*). Within the managed region, the eigen-analysis of selection ratios suggested selection was variable between individuals, with two axes needed to explain 91% of the variation. The first axis (64%) represented 7 individuals selecting both young and cut reed, while the second axis (27%) represented 3 birds selecting specifically young reed when foraging. In the unmanaged region birds selected old reed consistently (first axis explained 80% of the variation). Edges were consistently avoided.

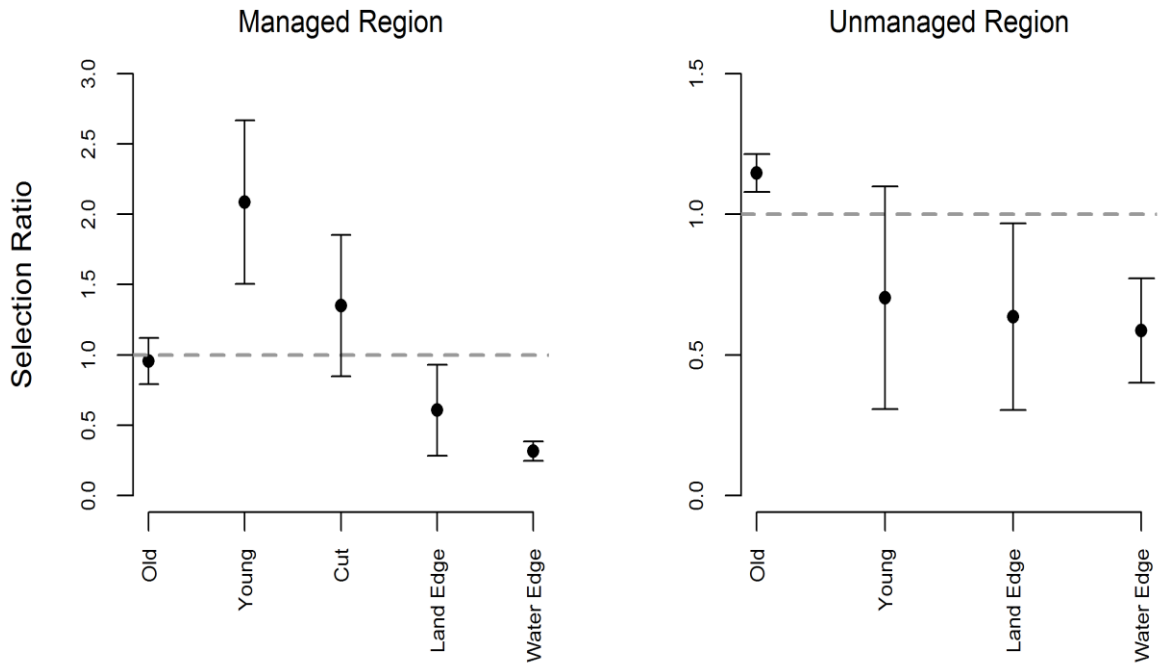


Figure 4.4 – Global selection ratios and 95% CIs of foraging trips undertaken by Bearded Reedlings in managed and unmanaged regions of the reedbed during the breeding season. No cut reed was available in the unmanaged region during either breeding season. Selection ratios above 1 indicate preference, while those below 1 indicate avoidance.

4.4.5 Habitat data and invertebrate analysis

We conducted measurements of the reed characteristics at 1124 points; 473 in old areas of reed, 193 in young areas, 205 in cut areas, 124 at the land edge and 129 the water edge. The linear models suggested there were considerable differences in structure between the reed categories (*Table 4.5*). Cut reed had an increased density and seed index when compared to old reed, but grew back with a significantly reduced height, diameter, stagger rating, leaf litter and water cover. Young reed was similarly shorter, denser and thinner than old reed, but showed an increased water cover. Reed at the land and water edge was higher and less dense than old reed. The land edge showed a reduced water cover while the water edge showed a reduced leaf litter. Only two variables changed seasonally, with a lower seed index occurring in the breeding season, and higher water cover in the winter. We saw no differences in the abundance of arthropods (ANOVA: $F_{4, 15} = 0.41$, P=0.8) or Nematocera ($F_{4, 15} = 0.42$, P=0.8) between the habitat categories.

Reed characteristics and invertebrate abundance within the habitat categories showed similar values between managed and unmanaged regions (*appendix 4.i*), apart from water cover which was increased in the unmanaged region in old ($T_{70.7}$=-5.17, P<0.001), young ($T_{50.7}$=-3.06, P<0.001) and water edge ($T_{10.9}$=-3.91, P<0.001) categories.

	Height	Density	Diameter	Seed Index	Stagger	Leaf Litter	Water Cover
Intercept	248.3 ±3.71	23.68 ±0.8	7.09 ±0.16	174.83 ±13.77	2.49 ±0.19	3.55 ±0.15	2.97 ±0.27
	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001	P<0.001
Reed Category (Old reed as reference level)							
Young	**-33.92 ±2.9**	**3.44 ±0.63**	**-0.54 ±0.12**	12.22 ±10.98	-0.06 ±0.14	0.1 ±0.12	**0.53 ±0.21**
	P<0.001	**P<0.001**	**P<0.001**	P=0.26	P=0.63	P=0.39	**P<0.001**
Cut	**-62.26 ±2.82**	**4.11 ±0.61**	**-1.77 ±0.12**	**79.52 ±10.77**	**-1.58 ±0.14**	**-1.57 ±0.11**	**-0.79 ±0.21**
	P<0.001	**P<0.001**	**P<0.001**	**P<0.001**	**P<0.001**	**P<0.001**	**P<0.001**
Land Edge	**8.28 ±3.43**	**-2.31 ±0.74**	0.28 ±0.14	-19.28 ±12.86	-0.1 ±0.14	0.28 ±0.14	**-0.81 ±0.25**
	P<0.001	**P<0.001**	P=0.053	P=0.13	P=0.46	P=0.05	**P<0.001**
Water Edge	**8.91 ±3.39**	**-2.89 ±0.73**	-0.08 ±0.14	2.31 ±12.73	0.17 ±0.15	**-0.81 ±0.14**	0.08 ±0.25
	P<0.001	**P<0.001**	P=0.55	P=0.85	P=0.27	**P<0.001**	P=0.73
Season (Autumn as reference level)							
Breeding	-1.13 ±3.59	-1.81 ±0.78	-0.24 ±0.15	**-44.53 ±13.23**	0.18 ±0.18	0.06 ±0.15	0.06 ±0.27
	P=0.75	P=0.06	P=0.12	**P<0.001**	P=0.32	P=0.65	P=0.79
Winter	-6.03 ±3.88	-1.17 ±0.84	0.04 ±0.16	-26.58 ±14.22	0.26 ±0.19	0.28 ±0.16	**0.9 ±0.29**
	P=0.12	P=0.16	P=0.8	P=0.06	P=0.17	P=0.08	**P<0.001**

Table 4.5 – Estimates ± standard error and P-values of habitat variables between the main reed categories. P-values are based on t-statistics. Significant terms are shown in bold.

4.5 Discussion

During the breeding season, we saw little evidence that reed cutting had an effect on the distribution of birds throughout the reedbed. The population level survey suggested a higher density of Bearded Reedlings around cut patches in the 2013 breeding season only. In the 2014 and 2015 breeding seasons the density of birds between cut and uncut patches was similar. This was verified in the design 2 breeding season analysis, which suggested that, when all reed categories are equally available to each individual, during the breeding season, birds would show avoidance of the reedbed edges, but had no preference between old, young and cut reed. The lack of selection between these latter categories was driven by the tendency for birds in the unmanaged region to utilise old reed, while birds from managed areas incorporated the presence of young and cut reed into their home ranges. Thus, our results provide no evidence that mosaic winter reed cutting has an effect on the overall breeding abundance or distribution of Bearded Reedlings throughout the reedbed.

Other studies have noted considerable impacts of reed cutting on breeding bird abundance. For example, Graveland (1999), shows increased densities of nesting Acrocephalus Warblers in uncut patches of a large reed stand in the Netherlands. Similarly, differences between distinct reedbeds have been noted, with Poulin and Lefebvre (2002) demonstrating a higher abundance of Bearded Reedlings in unmanaged reedbeds. These may be driven by structural changes in the reed (Valkama *et al.* 2008), invertebrate abundance (Ditlhogo *et al.* 1992, Schmidt *et al.* 2005) or the lack of suitable breeding habitat prior to regrowth (Graveland 1999). These previous studies concern commercial management where large blocks of reed are cut to maximise harvesting efficiency. Our study offers important insight into the effects of mosaic reedbed management and suggests this form of management has no impact on the relative density of breeding Bearded Reedlings throughout the reedbed. This is likely to be due to the preservation of large patches of old reed in both management regimes, which offers vital nest site habitat.

Despite no overall selection for managed areas in the higher orders, the design 3 analysis suggested the management regime had an impact on the fine-scale foraging decisions of Bearded Reedlings. These birds can undertake foraging trips of up to 500m (Poulin *et al.* 2000, Beemster *et al.* 2010), suggesting targeted resource selection. In the managed region we saw a marked selection during foraging trips for young reed that had remained uncut for between one and five growing seasons. However, this selection was not preserved between regions, with individuals in the unmanaged region foraging in old patches of reed, despite young reedbed being available in all individual home ranges. These between site differences in selection decisions may be explained by

changes in the arrangement of the overall habitat. In the managed region patches of young reed were invariably short strips, bordered by large patches of cut reed (*Figure 4.1*). In the unmanaged region, cut reed was absent and young reed surrounded by dense, old reed. Field observations in the managed region revealed that birds used the edges of the young reed strips for cover between brief forays into the cut patches. Thus, differences in selection between the management regimes can be well explained by the presence of cut areas.

Regardless of this specific selection, both young and cut reed after regrowth showed similar changes in structure in relation to old reed. These patches had shorter, thinner stems which grew back at a considerably higher density. Stems in these categories also tended to stand upright. Beemster *et al.* (2010) note the importance of recently grazed, early successional stages of reed for foraging Bearded Reedlings, suggesting that these sites offer increased invertebrates and a reduced structural complexity that may make prey easier to locate. We found no difference in invertebrate abundance between the habitat categories, but a clear selection for young and cut sites in the managed region. Reedbed habitat requires specific adaptations to allow proficient navigation. For example, Romero-Pujante *et al.* (2005) demonstrate that the length of the tail of the Bearded Reedling can dictate their ability to move efficiently between stems. The erect, thin reed stems in the cut and young reed may make it easier for birds to navigate and manipulate the habitat, increasing foraging efficiency and explaining the clear selection towards these reed types in the managed region.

In the unmanaged region, birds foraged within extensive areas of old reed. The increased distances of foraging trips in this region, however, still suggested specific selection of resources. All habitat categories in the unmanaged region were wetter than those in the managed region. Bibby (1981) shows that Bearded Reedlings in several reedbeds throughout England foraged in wet areas during the summer, with similar patterns recorded in other European reedbeds (Hoi and Hoi 2001, Beemster *et al.* 2010). These areas provided effective foraging on emerging Diptera (Bibby and Lunn 1982, Beemster *et al.* 2010). Patches of old reed with high water cover in the unmanaged region may have offered similar opportunities. Unfortunately, due to the inaccessibility of the reedbed, and extensive spatial variation in habitat structure, we could not accurately map the positions of the wettest areas from the ground. Remote sensing methods are beginning to have a role in highlighting fine-scale differences in apparently homogeneous habitats (Besnard *et al.* 2015) and should eventually offer an effective means to map characteristics of reedbed habitats (Poulin *et al.* 2010, Davranche *et al.* 2013), overcoming restrictions imposed by accessibility.

Overall, the results suggest that mosaic winter reed cutting does not impact on the distribution of breeding Bearded Reedlings throughout the reedbed, but may alter fine-scale foraging decisions. Our results also suggested that foraging trips and home range sizes were lower in the managed region. While this may indicate more efficient foraging in mosaic managed areas, comparative data on feeding rates and nest success between management regimes would offer further important insight. However, such data are difficult to collect for elusive species in sensitive habitats.

The results also offered critical information about the resource selection of this species in the non-breeding season. In order to exploit reedbed habitats during the winter, the Bearded Reedling alters the structure of its gut and ingests grit allowing it to forage on reed seeds (Spitzer 1972, Bibby 1981, Wilson 2014). This change occurs in September (Wilson 2014) with highest consumption of reed seeds occurring between November and January (Bibby 1981). Beemster *et al.* (2010), show that wintering populations in the Netherlands occupied areas of reed which had undergone grazing, as these sites offered increased seed abundance. We similarly expected birds to occupy areas of high seed abundance, which in our study were cut patches, during the autumn and winter. However, the winter population surveys showed consistently higher densities of birds in uncut habitat during both surveyed winters. Additionally, the radio tracking data showed explicit selection of old reed habitat during the autumn. This effect was consistent between individuals, and management regimes. It was, however, not reflected in the autumn population level surveys, possibly due to low sampling effort causing high variation in density estimates. The clear preference for old reed in the non-breeding season may be driven by the significantly increased leaf litter depths in these patches. Several studies suggest litter is an important winter foraging resource for Bearded Reedlings, which may continue to locate overwintering invertebrates in the detritus, or benefit from the consistent fall of reed seeds into the litter (Wawrzyniak and Sohns 1986, Surmacki and Stepniewski 2003, Wilson and Peach 2006).

In all the orders of habitat selection and throughout the season, we saw a clear avoidance of reed within 20m of either edge of the reedbed. This is in contrast or previous studies, which suggest a positive association of Bearded Reedlings with edges (Báldi and Kisbenedek 1999, Moskát and Báldi 1999), and the tendency for these birds to forage at the boundaries of pools (Bibby 1983, Beemster *et al.* 2010). In our system edges showed no dramatic changes in structure or reduction in insect or seed abundance, which may have driven avoidance or preference. Thus, the avoidance of these areas may have been the result of changing predation rates. Several studies have shown increased nest predation rates at reedbed edges (Chapter 5, Batáry *et al.* 2004, Báldi and Batáry

2005), but it is unclear whether these persist into adult predation rates. Our results suggest further research is needed to understand potential trade-offs between food abundance and adult predation rates at reed boundaries, especially as management schemes can influence the shape and size of reedbeds (Orłowski and Górka 2013).

Applying these results to reedbed management, we recommend winter mosaic reed cutting as a means to compromise between conservation interests and harvesting for either economic purposes or to rejuvenate reed growth. During the breeding season, this form of cutting should retain adequate stands of old, uncut, reed for birds to nest in, and patches of young or cut reed which look to provide effective foraging sites. Additionally, the importance of young reed in the managed region suggests a rotational, or temporally diverse management regime (Deák *et al.* 2015) that offers increased heterogeneity in the age structure of the reedbed, should benefit breeding birds. We also encourage conservation management to consider potential seasonal variation in habitat use, with the winter study suggesting areas of old reed, which are characterised by deep litter layers, provide critical winter resources for this species. Overall, this research provides the first insight into individual level space use of a highly specialised reedbed passerine. These data help clarify the effects of mosaic winter reed cutting for reed birds, and contribute directly to the debate surrounding the appropriate management of these habitats.

4.6 Acknowledgements

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4.7 Appendix 4i – *Comparison of habitat characteristics between managed and unmanaged regions. Tests conducted for each habitat category individually. P-Values are based on T tests.*

	Managed	Unmanaged	t	df	P Value
Old Reed					
Height (cm)	241.57	245.15	-0.73	83.92	0.55
Density (stems)	20.98	21.53	-0.47	72.70	0.64
Diameter (mm)	6.78	6.77	0.03	81.19	0.97
Seed Index	133.94	162.13	-1.27	80.61	0.21
Stagger (1-5)	2.75	2.85	-0.35	35.57	0.72
Leaf Litter (cm)	15.02	17.55	-1.91	69.60	0.06
Water Cover (%)	13.75	27.27	-5.17	70.72	<0.001
Young Reed					
Height	210.20	210.42	-0.05	72.45	0.95
Density	25.64	26.08	-0.31	52.84	0.76
Diameter	6.37	6.61	-0.65	51.88	0.52
Seed Index	150.91	153.23	-0.10	51.75	0.92
Stagger	2.36	3.21	-3.33	57.20	0.02
Leaf Litter	15.69	18.55	-2.38	62.31	0.03
Water Cover	18.42	28.68	-3.06	50.72	<0.001
Cut - too few data from unmanaged region for comparison					
Land Edge					
Height	261.16	247.30	1.11	11.83	0.29
Density	18.18	25.40	-2.71	11.42	0.02
Diameter	6.94	8.10	-2.84	14.28	0.02
Seed Index	114.99	150.80	-0.85	10.25	0.42
Stagger	2.75	2.85	-0.35	35.57	0.73
Leaf Litter	15.73	19.00	-1.11	11.69	0.29
Water Cover	8.91	15.50	-1.80	18.74	0.09
Water Edge					
Height	265.53	218.40	3.26	10.99	0.001
Density	18.82	20.40	-0.62	13.46	0.54
Diameter	6.90	6.57	0.81	15.31	0.43
Seed Index	154.75	163.64	-0.23	16.90	0.83
Stagger	3.00	2.50	0.89	7.93	0.4
Leaf Litter	13.18	19.50	-3.12	23.03	<0.001
Water Cover	10.09	33.00	-3.91	10.85	<0.001
Invertebrate Abundance					
Total Invertebrates	99.48	90.02	-0.25	15.04	0.81
Total Nematocera	21.54	20.70	-0.75	16.47	0.46

Chapter Five

The seasonal dynamics of artificial nest predation rates along edges in a mosaic managed reedbed

Iain Malzer, Barbara Helm

5.1 Abstract

Boundaries between different habitats can be responsible for changes in species interactions, including modified rates of encounter between predators and prey. Such 'edge effects' have been reported in nesting birds, where nest predation rates can be increased at habitat edges. The literature concerning edge effects on nest predation rates reveals a wide variation in results, even within single habitats, suggesting edge effects are not fixed, but dynamic throughout space and time. This study demonstrates the importance of considering dynamic mechanisms underlying edge effects and their relevance when undertaking habitat management. In reedbed habitats, management in the form of mosaic winter reed cutting can create extensive edges which change rapidly with reed regrowth during spring. We investigate the seasonal dynamics of reedbed edges using an artificial nest experiment based on the breeding biology of a reedbed specialist. We first demonstrate that nest predation decreases with increasing distance from the edge of cut reed blocks, suggesting edge effects have a pivotal role in this system. Using repeats throughout the breeding season we then confirm that nest predation rates are temporally dynamic and decline with the regrowth of reed. However, effects of edges on nest predation were consistent throughout the season. These results are of practical importance when considering appropriate habitat management, suggesting that reed cutting may heighten nest predation, especially before new growth matures. They also contribute directly to an overall understanding of the dynamic processes underlying edge effects and their potential role as drivers of time-dependent habitat use.

"Put all of your eggs in one basket, and then watch this basket"
Andrew Carnegie

5.2 Introduction

"Edge effects" are changes in ecological patterns that occur along the boundaries between different habitat types. They have been widely studied in a number of different habitats (Paton 1994, Crooks *et al.* 2004, Watson *et al.* 2004, Báldi and Batáry 2005) and several kinds of edge effects have been described (Murcia 1995). These may be abiotic processes, such as changes in microclimate with increasing distance from the habitat boundary (Chen *et al.* 1993), which in turn can have a direct consequence on the abundance and distribution of biological organisms along habitat edges (Guthery and Bingham 1992, Murcia 1995, Báldi 2005). Finally, changes in abundance or distribution of a given species along a habitat boundary may have indirect consequences for other organisms through an intensification or reduction in the chance of interactions between these species (Murcia 1995, Fagan *et al.* 1999).

Edge effects affecting species interactions have received considerable attention. For example, Fagan et al. (1999) suggest several mechanisms by which species interactions may be intensified along habitat edges. Organisms may show preferences for edges if they can exploit resources from both sides of the edge, encouraging them to spend more time at edges than in interior habitats (Suvorov *et al.* 2014). Similarly, when edges act as barriers animals often move parallel to them, treating them as 'travel lanes' (Fagan *et al.* 1999), which could result in increased interspecific contacts. 'Spillover' edge effects can further increase opportunities for species interactions. These occur where a species common in one environment moves to a neighbouring habitat where they interact with the species' resident in these areas (Rand *et al.* 2006). Such interactions will occur most frequently at the boundary becoming more dilute towards the interior.

An example of changing species interactions along habitat boundaries are avian nest predation rates, where proximity to an edge increases the probability of a nest being predated (Batáry and Báldi 2004). Increased predator activity along edges, and the spillover of predators into neighbouring habitats could provide mechanisms by which encounter rates between predators and nests are increased (Suvorov *et al.* 2014). As nest success is explicitly related to an individual's fitness, and is thus a vital demographic rate in bird populations (Fretwell 1972), edge effects on nest predation rates have been extensively explored. Many studies in forest and wetland habitats have found significant edge effects on nest predation (Paton 1994, Soderstrom 1999, Batáry and Báldi 2004), however, these results are far from unanimous (Lahti 2001, Vetter *et al.* 2013). It is therefore clear that the mechanisms underlying edge effects on nest predation are difficult to generalise between habitats, and that these processes are not fixed functions of edges but likely to vary both throughout space and over time (Paton 1994, Báldi 2005, Svobodová *et al.* 2012).

To gain a comprehensive understanding of the mechanisms underlying edge effects on nest predation rates, studies should consider, and where possible incorporate a means to test, the dynamic aspects of edge effects over time and space. This may be especially important for temporal effects which have received less attention than spatial variation. For example, changes in the abruptness and extent of edges over time may affect the tendency of animals to use them as travel lanes. Or, seasonally changing dispersive behaviours of predators may mediate movements into neighbouring habitats during spillover edge effects. This study seeks to demonstrate the significance of dynamic processes underlying edge effects on nest predation rates and emphasise the importance of the incorporation of temporal variation when defining an edge effect. We look to demonstrate these effects in managed reedbeds with the additional aim that results will contribute to conservation and management decisions at these important sites.

Reedbeds are a globally threatened habitat (Mitsch and Gosselink 2007) on which many specialist species rely (Cowie *et al.* 1992, Poulin *et al.* 2000). This includes several bird species which breed almost exclusively in these habitats (Hoi and Hoi 2001, Trnka and Prokop 2006, Trnka *et al.* 2014). Consequentially, edge effects have been well studied in reedbed habitats. Batáry and Báldi (2004) review studies in marsh habitats and demonstrate, overall, a significant edge effect on nest predation rates. However, subsequent experiments involving artificial nests have shown more variable results, suggesting effects may be dynamic (Batáry and Báldi 2005, Schiegg *et al.* 2007, Trnka *et al.* 2009, 2014, Suvorov *et al.* 2014, Jedlikowski *et al.* 2015). Indeed, several studies have alluded to dynamic spatial and temporal effects within reedbeds. Báldi and Batáry (2000) show that edge effects on predation rates vary between different sites. Further spatial variation may be driven by the sharpness of the edge (Angelstam 1986, Batáry *et al.* 2004). Seasonal (Hoi and Winkler 1994, Batáry *et al.* 2004, Schiegg *et al.* 2007), and longer term (Báldi 2005) temporal variation have also been noted.

In reedbed habitats, edges often result from human influence, being harvested commercially or managed for long term preservation (Hawke and Jose 1996, Poulin and Lefebvre 2002, Sathitsuksanoh *et al.* 2009, Trnka *et al.* 2014). Reed cutting can provide a resistance against the natural succession of the reedbed (Hawke and Jose 1996). It may also benefit breeding birds by increasing heterogeneity in the reedbed, providing birds with old reed in which to nest, and more open foraging sites (Hawke and Jose 1996). However, there are potential negatives (Valkama *et al.* 2008), with some literature suggesting a reduced arthropod and bird abundance after cutting (Poulin and Lefebvre 2002, Schmidt *et al.* 2005, Trnka and Prokop 2006). Recently, reedbed cutting practices have been undertaken in a mosaic pattern, with only small unconnected patches of the

reedbed being cut. This practice will hinder succession, while avoiding the implications for wildlife of cutting on a large scale (Trnka *et al.* 2014).

These mosaic managed reedbeds offer a useful system in which to study dynamic edge effects. Visually, reedbeds are uniform in structure, being composed mainly of uninterrupted *Phragmites* stems. Such stands can cover vast areas with this apparently homogeneous habitat with the consequence that edges within reedbeds, such as those caused by reed cutting, are especially apparent. Further, the effects of these cut edges within reedbeds will be extremely temporal. Most commonly, dead reed stems are cut in the winter months, generating open patches prior to the growing season, which start to be filled in by reed growth beginning in mid April. By June mature new reed will have reoccupied patches cut the previous winter (Hawke and Jose 1996, Stance 2010). Thus, in this system, the severity of edges caused by reed cutting is expected to vary dramatically throughout the breeding season of reedbed specialist Passerines, and currently, the implications of this for their breeding biology are not well established. Further study of predation rates in reedbeds can thereby contribute to understanding dynamic edge effects in general, but is also of considerable conservation value.

The Tay Reedbeds in Scotland are cut in a mosaic pattern to promote the breeding success of the most important population of Bearded Reedlings, *Panurus biarmicus*, in the British Isles (Peach 2000). This specially protected species is highly localised to reedbed habitats (Robinson 2005, Eaton *et al.* 2009) and may be especially susceptible to the effects of dynamic edges in mosaic managed reedbeds. It begins breeding in early April, having several broods until August (Cramp and Perrins 1993) and will therefore be nesting during every stage of new reed growth. In April, before new growth, nests are positioned in patches of dead reed stem, often close to habitat boundaries (Hoi and Hoi 2001) such as those between cut and uncut patches. If predation rates are mediated by edge effects along these boundaries, then the temporal changes in the structure of the reedbed over the season, should drive a dynamic, declining edge effect.

We use an artificial nest experiment conducted at the Tay Reedbeds to investigate this potentially dynamic edge effect caused by mosaic reedbed management. Artificial nest experiments have been useful when highlighting patterns in nest predation rates throughout different habitats (Soderstrom 1999, Batáry *et al.* 2004). They may also be especially important in reedbed habitats when access to real nests can cause considerable disturbance to nesting habitat. However, they can be misleading and subject to bias (Major and Kendal 1996, Zanette 2002, Moore and Robinson 2004). To mitigate these problems, this study followed the guidelines proposed by Major and Kendal (Major and Kendal 1996). At no point are quantitative comparisons drawn between

predation rates of artificial nests and real nests. Also, steps are taken to avoid induced predation of artificial nests (Skagen *et al.* 1999, Rangen *et al.* 2000, Purger *et al.* 2012). Finally, the experiments were based explicitly on the Bearded Reedling, this included imitating the design of the nest, the egg structure, the laying or placement dates, the number of broods and the incubation period.

To demonstrate this dynamic edge effect we test three hypotheses; **i)** that there is an edge effect on predation along the cut and uncut boundaries between patches of mosaic cut reedbed as measured by increasing nest predation rates closer to these edges. **ii)** That nest predation rates change over the season in association with seasonally changing characteristics of the reedbed habitat. And finally, **iii)** that edge effects on predation rates along cut and uncut boundaries are dynamic throughout the breeding season, being more pronounced early in the season, when edges are most apparent, than later in the season when reed growth is mature. This is tested by observing whether any edge effect is dependent on the level of new growth over the season. In addition to the investigation of dynamic edges in reed habitats, we also aim to assist practical reedbed conservation and management by identifying the more static characteristics of the reed that influence predation rates, such as reed density or height. This study aims to contribute to a general understanding of the mechanisms underlying dynamic edge effects, while providing relevant insight for the practical conservation of reedbed Passerines.

5.3 Materials and Methods

5.3.1 Study Site

The study took place during April-June, 2013 and 2014, in the Tay Reedbeds on the northern side of the Tay Estuary, Scotland (56°23.00', -003°10.00'). All permissions of access were granted by private land owners. The research was conducted in a protected habitat during the breeding season of several specially protected bird species. All appropriate Schedule 1 licences were granted by the British Trust for Ornithology and held by field researchers for the duration of the study. At around 4.1km^2 these are the largest *Phragmites* reedbeds on the British Isles. During January to March of each year in the study, reed blocks were cut using a Saiga reed harvester. The cut blocks were relatively uniform in size at around 350m^2. They were cut in a mosaic pattern with 50-100m of uncut reed between blocks and a minimum of 20m boundaries at the land and water edges. The same blocks were cut in each year apart from three larger blocks towards the west of the reedbed which were only cut in 2013.

5.3.2 Artificial Nest Design

The artificial nests were modelled on a small collection of Bearded Reedling nests from the Tay Reedbeds and Leighton Moss. A bowl shaped base made of 25x25mm chicken wire provided structure for the nests. Small *Phragmites* stems were woven through the wires to form the main structure. Larger stems and *Phragmites* leaves were positioned at the furthest edges. The cup depression in the centre of the nest, in which the eggs would be placed, was lined with *Phragmites* panicles, it had a circumference of 5cm and was around 6cm deep (see supporting information 1).

Four eggs were placed in each nest. Three of the eggs were made of white, oven drying, clay. Bearded reedling eggs are white with small black markings. We left the eggs fully white, as the benefits of adding these small markings are likely to be outweighed by the biases to predation incurred from unnatural paint scents (Rangen *et al.* 2000). The clay eggs were around 20mm from the apex to the base and had a 14mm circumference at their thickest width (Surmacki *et al.* 2003). The eggs were slightly heavier than the weights expected for Bearded Reedling eggs (2.5g, 1.9g, respectively). If predated, clay eggs should show imprints of teeth, claw or beak marks, allowing some insight into the extent of avian or mammalian predation (Boulton and Cassey 2004). A real quail's egg was also added to each nest to provide insight into the size of the predator, where nests with predated clay eggs, but intact quails eggs, would suggest small predators (Fulton and Ford 2007). In addition, nest cameras were positioned on 8 (5%) randomly chosen nests throughout the study, to record predation events and aid predator identification.

A nest was considered predated if any of the eggs were removed or there were obvious signs of predator interest such as marks or cuts on the clay eggs or the breaking of the quail eggs. After the experimental duration, if a nest was still intact it was considered not predated. Nests, eggs and cameras were left outside in a sheltered location for at least 5 days prior to their experimental placement to allow adequate 'airing' of the equipment before use (Small and Hunter 1988). Initial nest placement was conducted at dusk. This meant that any potential visual predators would have minimal time to relocate the nests before darkness if they should associate researchers with a food source. Subsequent nest checks were not limited to the evening, they occurred randomly during different periods of the day without any routine. In addition, rubber boots were worn and eggs were handled with gloves to minimise human scents.

5.3.3 Temporal Design

Replicates of the experiment were conducted in April and June in 2013, and April, May and June in 2014. The experiment was not conducted in May 2013 due to logistical constraints. We timed the placement of the nests in April with evidence that the birds were in breeding condition from bird ringing studies. We repeated the experiment in May to correspond with estimated laying times of late first or early second broods. We then repeated the experiment in June when the majority of second clutches are expected to have been laid. All nests within each month were placed on the same day and left for 12 days, which is the typical incubation period for the bearded reedling (Cramp and Perrins 1993). Between years, the dates of placement within each month were similar, to within 3 days. The design of the artificial nests was kept constant between each month and year. In one month, 16 nests were placed along the edges of two different cut blocks. This meant each experimental replicate consisted of 32 artificial nests placed at two distinct sites. Subsequent analysis suggested little variation in predation patterns between spatial replicates, and so in further analysis data were pooled between sites. Nests were checked every second day, meaning an artificial nest surviving for the full 12 days, would be checked 6 times.

The study therefore has three temporal axes. i) The year, either 2013 or 2014, of the experimental repeat. ii) The month of the repeat within a given year, measured as the number of days in the given year since April 1st and hereafter referred to as "April days". Finally, iii) the number of days during a given experimental repeat that the nest had been exposed for, hereafter "exposure days". On completion of all the experimental replicates over the two breeding seasons the fates of 160 artificial nests were available.

5.3.4 Spatial Design

In each year, the experiment was conducted simultaneously at the edges of two cut blocks. Due to slightly fewer locations being cut in 2014, we used different cut blocks in 2013 to those used in 2014. In 2013 cut blocks used in each experimental replicate were 1km apart, while in 2014 they were separated by 500m. All the blocks used were similar in size and had been cut in the previous winter using the same reed harvesting machine and technique. All sites had been cut yearly following this protocol for at least five years previous to the experiment.

The artificial nests were placed in old uncut reed at differing distances from the edges of the cut boundaries up to a distance of 14 metres. This distance threshold corresponds with the distances of several real nests located previously on the Tay (Malzer, personal observations). Other real nests have been located considerably deeper into the reeds, but due to the dense impenetrability of the uncut areas, any edge effects are likely to sharply decline with distance, and be captured within this distance threshold. 16 nests were placed between 0.0 and 7.0 metres from the edge, and 16 between 7.1 and 14.0 metres to ensure a uniform distribution of nests throughout the distance threshold. A random number between these boundaries generated in R 3.1.1 (R Development Core Team 2011) defined the distance of the given nest. Nests were placed every 10 metres along the cut boundary at a height of 30cm off of the ground. Placement of the nests along the edge of the cut area occurred in an alternating manner with one nest being placed between 0-7 metres, and the next between 7-14 metres. This ensured there were no clusters of nests at similar depths into the uncut reed when moving along the boundaries (See *Figure 5.1*).

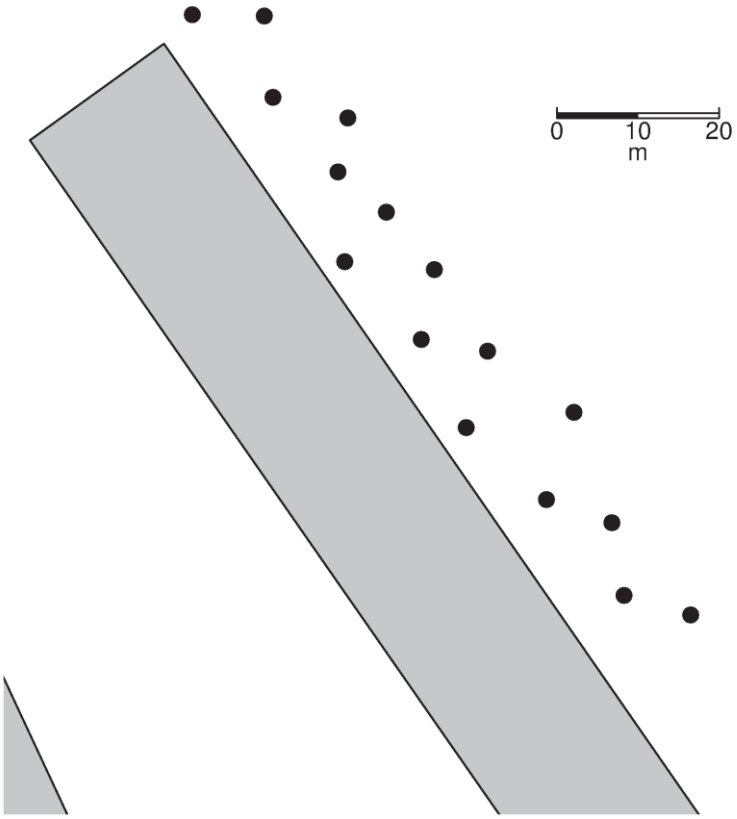

Figure 5.1 - Spatial layout of artificial nests along the boundary of a block of cut reeds. The dots represent artificial nest locations; the grey rectangles are cut patches of reed; remaining, unshaded areas are unmanaged reed. Example shown is for half the nests placed in April 2013.

5.3.5 Quantifying Habitat Characteristics

Two distinct habitat characteristic datasets were collected during the study. Data were first collected from random patches of cut and uncut reed almost weekly throughout both seasons. This allowed the growth of the reed to be quantified (*Figure 5.2*) and highlighted any differences between new growth in cut and uncut patches. Additionally, habitat measurements were also made around the artificial nest sites after the nest became inactive. The data collected around the

nest sites were used to quantify reed characteristics at each nest and used in subsequent analysis to model predation rates.

The reed characteristics were measured at each random point or nest using the following methods. The heights (in cm) of five randomly selected reeds within 1m of the point were measured to obtain the average heights around the given nest. Density was measured by inserting a 1m long stick into the reeds at a height of 1m and counting the number of stems touching the stick (Batáry and Báldi 2005). Again five measurements per point were taken to obtain average densities. These measures were conducted for both dead and alive stems. The sum of the density of dead and alive stems gave the overall density. The depth of the litter layer was measured in three locations around the point to the nearest 5cm. This was conducted by parting the litter until the mud below was visible and measuring the depth between the upper litter and ground below (Hulme 2008). Average water cover was estimated to the nearest 10% using a 0.5 x 0.5m quadrat in three locations within 3m of the artificial nest (Hulme 2008). Finally, a single number between 1 and 5 was used to categorise the degree of reed stagger around each nest. As the reeds age and areas become dense with multiple years of new growth, they often bend and, in some cases areas, can become quite flattened. Areas with straight, erect reeds were given a stagger rating of 1, while the flattest areas were classed as 5 (Tarr *et al.* 2004).

5.3.6 Statistical Analysis

The differences in habitat variables collected at artificial nest sites over the given season were investigated using linear models with April days as the predictor variable. Changes between the two years of the study were investigated using Mann-Whitney tests for leaf litter and water cover, which did not meet assumptions of normality, and using T-Tests for all other variables. When comparing the differences in new reed height and density between years, only reed measurements collected during April and June were analysed. Since these specific characteristics change so extensively through the season, including the May data, collected only in 2014, would invalidate the comparison. Finally, T-Tests were used to compare height and density of mature growth collected from different areas of the reedbed between managed and unmanaged sites.

To test whether there was a temporal effect on the survival probabilities of the artificial nests driven by the month in which the nest was active, we calculated Kaplan-Meier survival functions for nests in each month (Kaplan and Meier 1958). This is a simple measure of the proportion of nests surviving at each nest check over the duration of their exposure. We used month as a three level categorical variable, rather than April days, as these functions cannot

accommodate continuous variables. We used the nonparametric log-rank test to formally compare the survival distributions of the different levels of this covariate (Mantel 1966). This gave an indication of overall temporal effects on survival within a season.

We then used Cox's proportional hazards (CPH) models in the R package survival (Therneau 2014), to investigate the effects of a wider set of covariates on the tendency of an artificial nest to be predated. These semi-parametric models allow the probability per unit of time that an event will occur to be modelled as a function of a baseline hazard and a combination of either continuous variables, such as the distance from the edge of a cut area, or categorical variables, for example the year of nest placement. These survival analysis techniques have seen increasing use in nest predation studies in which the age of the nest at first encounter, and the age at failure are known (Brennan 2010, Leighton *et al.* 2011, Sarà *et al.* 2012, DiMaggio *et al.* 2013), with the major motive for their use being the well developed framework and readily interpretable output (Nur *et al.* 2004, Perry *et al.* 2008).

Several of the habitat variables, namely those concerning the characteristics of the reed, were correlated and therefore could not be included as separate covariates in the CPH models. We therefore used a principal component analysis (PCA) to reduce the dimensionality of the reed characteristic covariates (Hotelling 1933). Covariates included in the PCA were old height, new height, old density, new density and degree of stagger. These were standardised to have a mean of 0 and standard deviation of 1 before the PCA was carried out on the correlation matrix. The importance of each resulting axis was then assessed using a parallel analysis approach (R –Package paran, (Dinno 2012) where eigenvalues from the PCA were contrasted to those of 10000 simulations of normal, uncorrelated datasets with the same structure as the original data (Franklin *et al.* 1995). Scores from the axes deemed most important by the parallel analysis were then retained and used as continuous explanatory variables in the models.

A full CPH model was then fit including all the covariates in question, except for date which was correlated with reed regrowth. These were: the reed characteristics represented by the relevant principal component scores, water cover, leaf litter depth, distance of the nest from the edge of a cut area and the year of the study. We also included an interaction term between the principal component representing new growth (see results) and the distance from the edge of the cut area to investigate any changes in edge effects over the growing season. Adherence to the model assumption that the effect of a predictor is proportional over time, was assessed using Schoenfeld residuals (Fox 2002).

Starting with the full model, we used a backwards stepwise approach based on the AIC values of each candidate model to find the most appropriate models. This was conducted using the stepAIC command in R package MASS (Venables and Ripley 2002).

5.4 Results

5.4.1 Reed Growth and Phenology

Between April, May and June there was a rapid increase in the biomass of reed as new growth occurred (*Figure 5.2*). New growth led to an increase in the height (Linear Model; $F_{1, 158}$=256.9, P<0.001) and total density ($F_{1, 158}$=57.4, P<0.001) of new reeds over the season. *Table 5.1* shows the correlations between all the recorded covariates. The density and height of new reed growth showed a strong positive correlation with April days. The correlation between new height and new density was captured in the PCA. On completion of the PCA the parallel analysis for dimension reduction suggested the retention of the first three principal components. These accounted for 81% of the variation between the covariates concerning reed characteristics (*Table 5.2*). Principal component 1 (PC1) represented the new growth of reed, with low scores representing no new growth and the highest scores representing dense, high new growth. PC2 represented old reed density and the degree of stagger. PC3 represented old height only. Of the other habitat variables, water cover fell over the season at nest sites ($F_{1, 158}$=5.68, P=0.01), and leaf litter increased (Leaf Litter $F_{1, 158}$=4.96, P=0.026). There was a slight decrease in the height of the old growth ($F_{1, 158}$=3.61, P=0.056). The degree of stagger remained constant over the season (Stagger; $F_{1, 158}$=0.647, P=0.52).

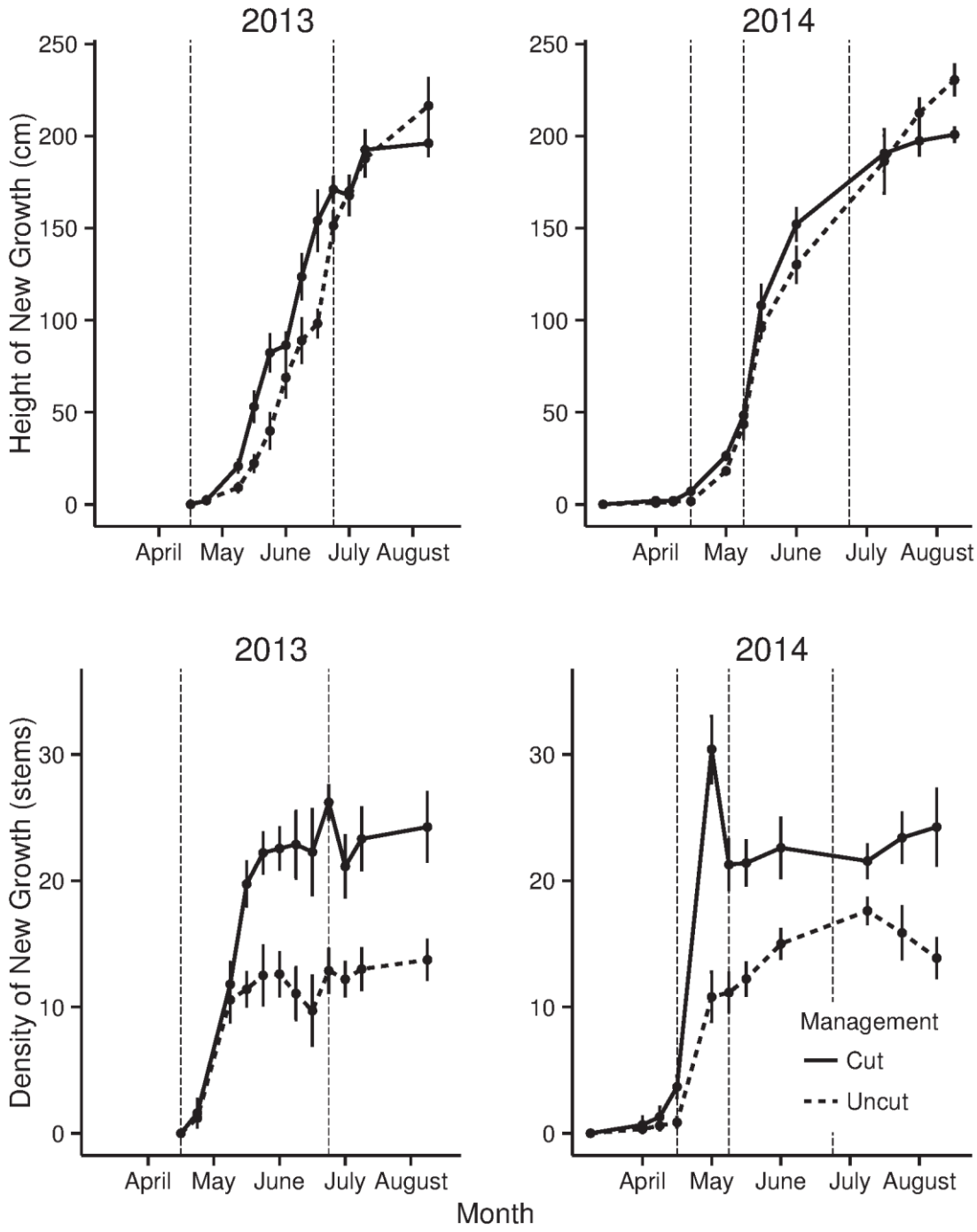

Figure 5.2 - Growth of new reeds. A) Average height and B) density of new reed stems in each recorded week of the study in 2013 and 2014. Measurements were made on the same day for sites cut the preceding winter, and uncut reed. Vertical dotted lines represent the weeks in which the artificial nest experiments were initiated. Error bars are one standard error from the mean.

	Old Height	New Height	Old Density	New Density	Total Density	Water Cover	Leaf Litter	Degree stagger	Distance	April days
Old Height	1									
New Height	-0.21*	1								
Old Density	0.13	-0.19	1							
New Density	-0.22*	0.81*	-0.17	1						
Total Density	-0.05	0.44*	0.61*	0.60*	1					
Water Cover	0.19	-0.19	-0.02	-0.21*	-0.17	1				
Leaf Litter	-0.02	0.22	0.12	0.08	0.16	0.05	1			
Degree Stagger	0.06*	0.05	0.18	0.02	0.16	0.03	0.25	1		
Distance	0	0.14	0.16	-0.02	0.11	0.02	0.28*	0.19	1	
April Days	-0.15	0.89*	-0.08	0.79*	0.51*	-0.18	0.17	0.08	0.07	1

Table 5.1 - Correlations between habitat covariates. Numbers represent Pearson's r correlation coefficients. Significant correlations (P<0.01) are marked with an asterisk.

Reed Characteristic	PC1 (0.40)[a]	PC2 (0.23)	PC3 (0.17)
Height of Old Reed	-0.324	0.224	0.916
Height of New Reed	0.639	0.198	0.175
Density of Old Reed	-0.280	0.558	0.289
Density of New Reed	0.637	0.189	0.157
Degree of Stagger	-0.023	0.750	0.145

Table 5.2 – Factor loadings of the first three principal components included in the further analysis. [a] Numbers in brackets are the proportion of variation in the dataset that each principal component explains.

Figure 5.2 shows the differences in reed growth between areas of reed that were cut the preceding winter, and uncut reed. New growth in cut areas reached a lower maximum height (cut sites: 217.16, uncut sites: 241.25 cm, $T\text{-}Test_{1, 137}$=-5.37, P<0.001), and higher density (cut sites: 27.6 uncut sites: 22.2stems, $T\text{-}Test_{1, 152}$=-6.95, P<0.001) when mature than in uncut areas. The growth curves show that the final artificial nest experiments in June were conducted when reed was at two thirds of its maximum height.

There were differences in the phenology of new reed growth between the years of the study. In 2013 new growth appeared suddenly in mid April and rapidly increased in biomass over the growing period (*Figure 5.2*). New growth appeared around five weeks earlier in 2014, but remained at low height and density until mid April when rapid growth occurred. This meant that, despite new shoots appearing far earlier in 2014, the major growth periods were similar between the years. Of the habitat covariates collected at the sites of artificial nests, only the depth of the leaf litter differed between the years of the study (*Table 5.3*).

Covariate	2013	2014	T / W Value	P-Value[a,b]
Old reed height (cm)	223.37	228.05	-0.817	0.415
New reed height (cm)	61.44	82.4	-1.099	0.27
Old reed density (no. stems)	18.52	19.57	-1.452	0.148
New reed density (no. stems)	5.16	4.3	1.105	0.271
Total reed density (no. stems)	23.6	23.8	-0.174	0.862
Degree of stagger	2.18	2.39	-0.947	0.344
Water Cover (% of quadrat)	*14.5*	*18.2*	*2657.5*	*0.137*
Leaf Litter (cm)	*11.48*	*17.0*	*2171*	*0.001*

Table 5.3 – Differences in habitat variables collected around artificial nest sites during April and June, between years of the study. P-values were calculated using T-Tests for normally distributed variables. The final two variables, in italics, did not conform to normality and so P-values are based on Mann-Whitney U tests, with W values as the test statistics. [a] P-values were calculated using T-Tests for normally distributed variables. [b] The final two variables, in italics, did not conform to normality and so P-values are based on Mann-Whitney U tests, with W values as the test statistics.

5.4.2 Nest Predation

Overall 53% of the artificial nests placed throughout the study saw a predation event. 2013 saw fewer nests predated (31.2%) than 2014 (68.75%) (*Figure 5.3*). When pooling the nests over years, April saw a higher proportion of nests predated (71.8%), than May and June (62.5%, 31.2%, respectively). The Kaplan-Meier survival functions showed a decrease in the proportion of nests predated over the months of the study (Log-Rank Test; DF=2, χ^2= 23.1, P < 0.001) (*Figure 5.4*). *Table 5.4* details the hazard ratios and the P-Values of the covariates included in the full Cox proportional hazards model and highlights the most important covariates after the backward stepwise model selection procedure. The most important covariates were the distance of the nest from the edge of the cut area, PC1, PC2 and the year of the study. The only identified predator was a water rail, *Rallus aquaticus*, which was recorded taking a quail's egg (supporting information 2). There was no evidence of mammalian predation on either of the nest cameras or from teeth or claw marks left upon the clay eggs. Unfortunately, no further information could be collected from the clay eggs, as on predation events they tended to be left intact or removed from the nest completely.

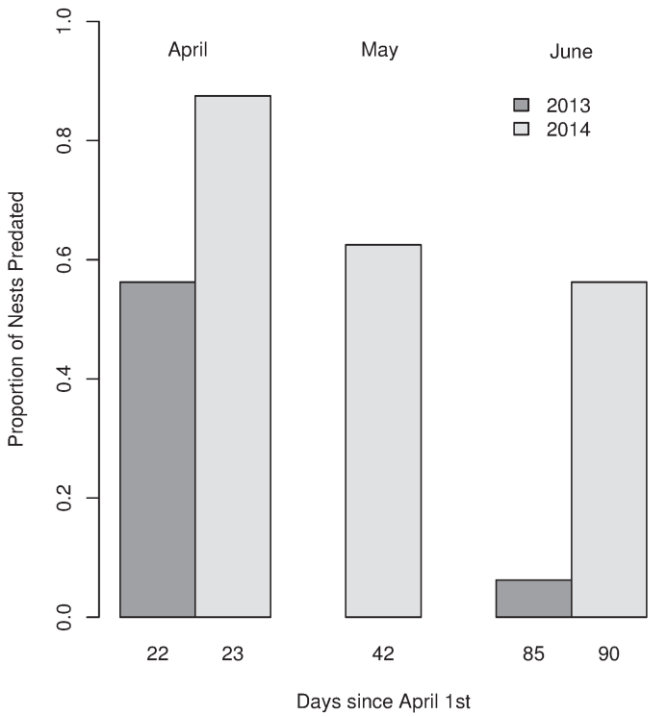

Figure 5.3 - Proportion of nests predated during each experimental repeat and the number of days since April 1st that the repeat was conducted.

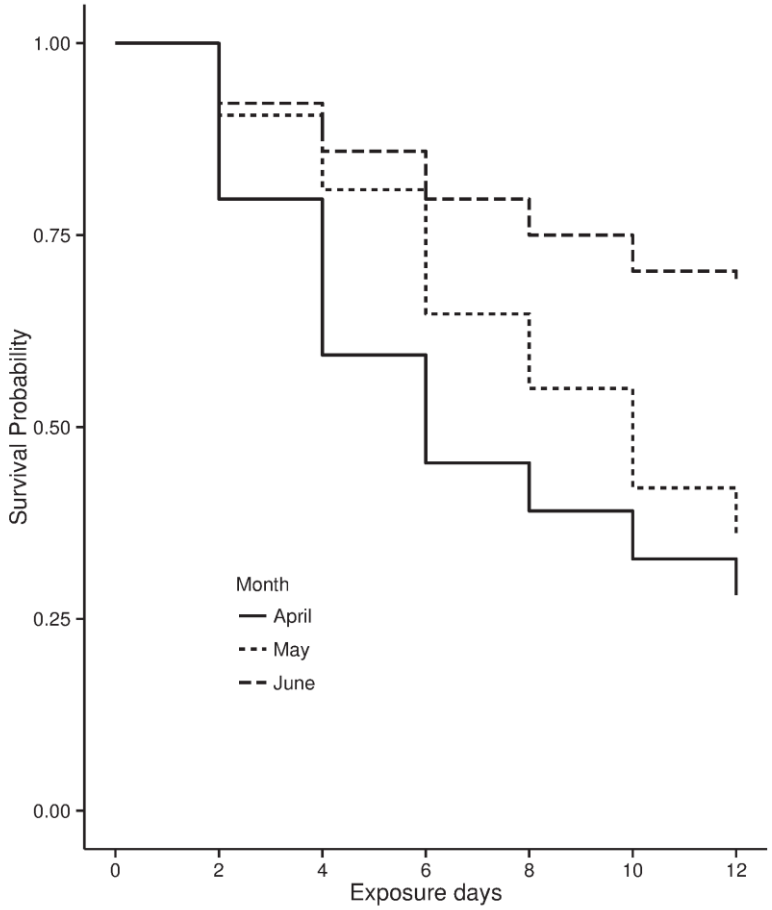

Figure 5.4 - Kaplan-Meier survival functions for nests placed in April, May and June

Covariate[a]	ΔAIC[b]	Hazard Ratio	95% CI	Wald Statistic	P Value
PC2	**0**	**0.57**	**0.47-0.71**	**-5.30**	**< 0.001**
PC1	**0**	**0.62**	**0.52-0.74**	**-5.23**	**< 0.001**
Year	**0**	**6.4**	**3.64-11.39**	**6.42**	**< 0.001**
Distance	**0**	**0.91**	**0.86-0.97**	**-3.13**	**0.0017**
PC3	**0**	**0.83**	**0.65-1.05**	**-1.15**	**0.12**
Leaf Litter	1.68	1.00	0.98-1.03	0.57	0.57
Distance:PC1 (Interaction)	1.28	1.00	0.95 -1.04	-0.36	0.72
Water Cover	2.00	0.99	0.98-1.01	-0.20	0.84

Table 5.4 – Hazard ratios, associated 95% CIs, Wald Statistics and P-values of all the effects included in the full model. [a] Terms included in the most supported model are shown in bold. [b] ΔAIC values are the difference between the AIC of the most supported model and the same model including the effect in question.

5.5 Discussion

We tested three hypotheses with the aim to demonstrate the importance of considering dynamic edge effects in mosaic managed reedbed systems. We first established the presence of an edge effect on nest predation along the edges of cut patches of reed. The most supported CPH models predicted a significant reduction in predation rates with increasing distance from the edge of the cut area. Several other studies have demonstrated similar effects along a variety of natural edges within reedbeds (Batáry *et al.* 2004, Báldi 2005, Báldi and Batáry 2005, Schiegg *et al.* 2007). This edge effect is likely to be driven by a change in species interactions where there is an increase in the rate of encounter between predators and nests along the cut and uncut boundaries.

Such increased encounter rates could occur through several mechanisms. Suvorov *et al.* (Suvorov *et al.* 2014) suggest that spillover of predators would explain the existence of edge effects in reedbeds if predation rates in neighbouring habitats and at the boundary were higher than in reedbed interior. Alternatively, predation rates that become more dilute towards the interior of both habitats would suggest higher predator activity at boundaries. Since cut reed at low stages of growth does not offer adequate nesting habitat (Valkama *et al.* 2008, Trnka *et al.* 2014), we could not compare predation rates in both cut and uncut habitats, but found a clear increase in survival with distance into the reedbed. We suggest that a combination of both spillover mechanisms and boundary attraction could drive edge effects in mosaic cut reedbeds. Neighbouring habitats, such as farmland in this study, can support complex predator communities (Crick *et al.* 1994) that may move into the cut areas when accessible. In addition, edges in the study system were non-gradual, with cut reed bordering on old, homogeneous uncut reed, as confirmed by a lack of correlation between habitat variables and distance from the edge. The edges of cut areas will therefore present a dense barrier of reeds to many predatory species, potentially increasing movements parallel to the boundaries (Crabtree *et al.* 1989, Picman *et al.* 1993).

We then established whether nest predation rates changed consistently over the season in the two years of the study. The seasonal repeats clearly identified a seasonal decline in artificial nest predation rates (*Figures 5.3, 5.4*). This seasonality was best modelled through new reed growth (PC1). *Phragmites* reedbeds at temperate latitudes begin new reed growth in April, maturing by June or July (Stance 2010). This meant that during the nest experiments undertaken in April, cut squares were accessible with no new reed biomass. By June new growth was dense and around two thirds of its height at full maturity. The changing accessibility of the reedbed through the cut patches could therefore be a major driver of predation rates. Further, Batáry *et al.* (2004) show a reduction in nest predation rates as new reed growth occurs and suggest nests are more difficult to

find when new growth is mature. We suggest that new reed growth both reduces the accessibility of the cut areas to predators and makes nests more difficult for predators to locate, discouraging them from searching inefficiently in low payoff areas of dense, mature reed. In April, an increased accessibility will increase the rates of encounter between predators and nests along the boundaries of cut and uncut patches, while later in the season, reduced accessibility and more effectively hidden nests will decrease these encounter rates.

These results clearly stress the importance of considering dynamic processes when investigating nest predation rates and that the fitness implications of habitat use in this system may be time-dependent. Trnka *et al.* (Trnka *et al.* 2014), report no differences in predation rates in artificial reed warbler nests between cut and uncut reed stands in Slovakia. However, since comparisons between managed and unmanaged sites can only be made when reed is mature, as early growth does not offer adequate nesting sites, these results cannot consider effects over the full season. By using only the edges of cut areas, we were able to answer Trnka's (2014) call for an investigation into the effects of mosaic reedbed management on nest predation rates throughout the whole breeding season and demonstrate that such effects are temporally dynamic. Species such as the Bearded Reedling will begin breeding before reed growth has initiated. In several species, recruitment rates of early broods are higher than in later broods (Järvinen 1989, Verboven and Visser 1998, Graveland 1999, Møller 2002), making them vital for overall breeding productivity. Thus, increased predation rates of early broods in mosaic managed reedbeds could have important fitness implications for birds breeding in this habitat.

With the third hypothesis we aimed to demonstrate a dynamic edge effect in this system by observing the interaction between the effect of the distance from the edge of the cut boundary, and the temporally changing reed structure (PC1). If edge effects are intrinsically related to the accessibility of the reed, and this changes dramatically over the season, we would have expected edge effects to be accentuated in the earlier months of the study when there was no new growth in the cut areas. Despite the strong seasonal effects on predation rates, there was no statistical support for an interaction between distance from the edge and the extent of new growth (PC1). This suggested that any edge effects in this system had a consistent impact in each seasonal repeat and that the dense new growth did not diminish the importance of the boundary between previously managed and unmanaged reed. This edge effect was therefore less dynamic than originally expected, a result that directly emphasises the difficulties in predicting edge effects and the need for a full understanding of the study system when defining an edge effect.

For example, the reason for the unexpected consistency of the edge effect throughout the season in this system could be the continued structural differences between patches of cut and uncut reed even later in the season when reed is mature. The habitat data collected from areas outwith the nests demonstrated that there were considerable changes in the structure of reed between cut patches, and uncut reed when mature. In patches that had been cut reed grew back at a higher density and eventually to a lower height (Valkama *et al.* 2008). Therefore, the edges of the cut areas are likely to still be apparent to predators in June when reed is mature. Aerial predators such as the Marsh Harrier, *Circus aeruginosus,* are important predators in reed systems (Bensch and Hasselquist 1994, Hansson *et al.* 2000, Batáry *et al.* 2004, Báldi and Batáry 2005, Trnka *et al.* 2011) and could benefit from the inhomogeneity of cut mosaics when hunting. This effect could persist even with the less distinct boundaries at more mature growth. The study also suggested water rail can contribute to nest predation in this system. This species is a reed specialist, reported to prefer predating nests in the interior of the reedbed (Hansson *et al.* 2000). In our study, edges created by reed cutting are temporal boundaries within the interior of the reedbed and so water rail could be an important pressure, regardless of the state of reed growth.

Overall, the experiment provided little insight into the main predators of the artificial nests. Despite this, it is important to consider the changing behaviours of predators as potential causes of variation in predation rates. Some predator guilds can show an avoidance of research activity around nests (Richardson *et al.* 2009, Ibáñez-Álamo *et al.* 2012), which may explain the lack of evidence of mammalian predation in our study. However, as previous studies in reedbeds also show little mammalian nest predation (Hansson *et al.* 2000, Batáry *et al.* 2004), and overall nest predation rates were relatively high in this study, we suggest this potential behavioural bias is mitigated. Additionally, seasonal variation in predation rates may be driven by temporal changes in predator behaviour or community. Further identification of the main predators in this system is needed in order to establish the importance of temporal changes in predator behaviours, and how these affect nest predation rates.

While the results show both spatial and temporal dynamics have an important role in reedbed nest predation, we also identified more static aspects of habitat that were associated with nest predation. The reed characteristics represented in PC2 were the density of old reed and the stagger rating for the reed surrounding the nest. These qualities concern only the old, dead reed stems, and are therefore unrelated to both seasonal changes in reed structure and the distance from the edges. They normally occur together when several years of growth accumulate, with old dead stems eventually becoming flatter. Nests in the most dense and staggered reed patches saw lower

predation rates. This is probably due to the difficulties in locating nests within the most impenetrable, compacted areas of reed. Generally studies have shown an increase in survival of both real and artificial nests in the most dense areas of reed (Graveland 1998, Honza *et al.* 1998, Kleindorfer *et al.* 2003, Batáry and Báldi 2004, Trnka and Prokop 2006, Eising *et al.* 2008). However, few have combined this with a rating for reed stagger, which could have implications for aerial predators as these flattened areas obscure nests from above. These results highlight the importance of preserving such reed characteristics during management.

Although not directly investigated, the results also suggested a wider temporal dynamic in nest predation rates. 2014 saw higher predation rates than 2013. This may be explained by changing nest densities. Hoi and Winkler (1994) use artificial nests in reedbeds to demonstrate that predation rates increase as the density of nests increases. They suggest that when nest density is high, there is a higher payoff for predators during foraging (Batáry and Báldi 2004). While the number of artificial nests placed in each experimental repeat was consistent, Bearded Reedlings are renowned for fluctuating population sizes (Pearson 1975, Campbell *et al.* 1992, Wilson and Peach 2006). Despite similar ringing effort between years, total numbers of new Bearded Reedlings ringed on the Tay increased by over 150% between 2013 and 2014. Thus, the clear increase in predation rates could have been driven by more predators exploiting the higher density of breeding birds during 2014.

Another possible driver of changes in predation rates between years, may have been differences in the phenology of reed growth. In 2013 a cold start to spring delayed the initiation of reed growth, with new shoots not appearing until late April. In 2014, the reed shoots appeared at that start of April. This is unlikely to have invalidated comparisons of nest predation between years in this study, as the experimental repeats occurred when reed was at a similar growth stage in each year (*Figure 5.2*). Similarly, the only habitat variable that significantly changed with the year of the study was leaf litter, which, in further analysis, was seen to have little effect on predation rates. Clearly, further yearly repeats would assist our understanding of the long term changes in predation rates. These would also control for the potential that predation rates were biased during a given experimental repeat by a single predatory individual learning to exploit the artificial nests.

The results contribute to discussion concerning effective reedbed management. Management practices should consider both the benefits and disadvantages of reed cutting. Resistance against reedbed succession may offer long term stability of the reed stand (Hawke and Jose 1996, Trnka *et al.* 2014). Further, areas of new growth after reed cutting may offer effective foraging opportunities for birds (Poulin and Lefebvre 2002, Beemster *et al.* 2010). However, studies have shown a reduction in the numbers of many bird species in managed areas (Poulin and Lefebvre

2002, Poulin *et al.* 2002, Vadász *et al.* 2008), which may be driven by reduced invertebrate abundances (Schmidt *et al.* 2005, Valkama *et al.* 2008) or delays to breeding (Graveland 1999). A compromise may be found in the form of mosaic reedbed cutting which may preserve invertebrate abundance and impede succession (Trnka *et al.* 2014). We emphasise, however, that the edge effects on nest predation caused by mosaic cutting could have adverse effects for breeding birds, especially those breeding before new reed growth has matured, and that these effects should be considered in future managmenent.

The study shows that several factors contribute to the survival of artificial nests in mosaic cut reedbeds. These are a combination of spatial (edge effects), temporal (seasonal changes in the new reed growth), and static (the structure of the old reed) processes. Despite predictions, spatial edge effects were unaffected by seasonal temporal changes and so the edge effect itself was less dynamic than originally predicted. In natural systems, it is likely that birds have evolved to cope with increased nest predation rates at edges using traditional environmental cues to avoid them. For example, in reedbed systems, natural reed edges have clear gradients in reed density as the reedbed expands outwardly (Coops *et al.* 1996). Animals may be further adapted to cope with dynamic edge effects, if variation is consistent and predictable. Thus, it is essential that for systems subject to anthropogenic influence, where edges may be unpredictable both spatially and temporally, and where traditional environmental cues may be misleading (Schlaepfer *et al.* 2002), that we understand the implications of edges, and the dynamic processes underlying them.

5.6 Acknowledgements

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Chapter Six

Nest timing, nest site selection and nest structure in a high latitude population of Bearded Reedlings, *Panurus biarmicus*.

Iain Malzer, Mike Hansell

6.1 Abstract

Understanding the nesting habits of protected species can assist conservation in predicting the effects of environmental management. The Bearded Reedling, *Panurus biarmicus*, is a specialist reedbed Passerine. Its restriction to reedbeds and tendency to undergo wide population fluctuations, have made it a protected species in the UK, often at the centre of reedbed management plans. Despite this, only limited data are available on natural nesting habits of this species as, relative to more generalist species, nest locating can require higher effort. We seek to address this omission by monitoring a sample of Bearded Reedling nests from a population on the northern fringe of this species' range. First egg dates and brood sizes were consistent between years of the study despite variation in spring temperature. We quantify fine-scale nest site selection in relation to local reed characteristics, with Bearded Reedlings positively selecting dense, compacted and dry areas of the reedbed for nesting. Finally, we provide quantification of the nest structure in this species and demonstrate that both local nest site characteristics and temperature contribute to variation in nest dimensions. The results offer insight into the nesting habits of this specialist species, which can be directly incorporated into conservation and management decisions.

"Below this stane John Allan rests
An honest soul, though plain,
He sought all hail Sabbath day for nests,
But always sought in vane."

Alexander Wilson 1784

6.2 Introduction

Nesting is a vital stage in the annual cycle of a bird, being clearly linked to individual fitness and thus having consequences for the wider population (Streby *et al.* 2014). Understanding the nesting decisions of birds, and processes influencing these decisions, is fundamental when developing successful species conservation strategies. In rare or highly specialist species nesting information is often sparse as fewer nests are available to locate and subsequently monitor. As specialist species are often the most vulnerable to habitat modification or climatic change (McKinney 1997, Colles *et al.* 2009), studies which focus on collecting nesting information in these species are likely to provide relevant insight for conservation.

The Bearded Reedling, *Panurus biarmicus,* is an open cup nesting passerine highly specialised to *Phragmites australis* reedbeds. Information concerning the nesting habits of this species is limited in comparison to other, more generalist, species due to the Bearded Reedling's strict specialisation to reedbed habitats. Reedbeds are normally managed by harvesting or altering water levels in order to impede vegetative succession and preserve the long-term integrity of the reedbed (Hawke and Jose 1996, Poulin *et al.* 2002, Valkama *et al.* 2008). Commonly, reedbed management has the additional motive to provide high quality habitat for breeding birds (Hawke and Jose 1996, GIlbert *et al.* 2005). Understanding nesting decisions of reed specialist birds such as the Bearded Reedling, could therefore directly enhance these management regimes. Further, while the wide range of the Bearded Reedling has led to its categorisation as 'of least concern' on the IUCN's red list (BirdLife International 2014), it is a protected species in the UK (Eaton *et al.* 2009) infamous for rapid, and wide, population fluctuations (Wilson and Peach 2006), the causes of which may be associated with nesting.

Nesting birds must decide the timing of nesting, the selection of a nest site and the structure of the nest itself. By understanding the flexibility in the timing of breeding and nature of other nesting details, predictions can be made about the potential implications of climatic change. Nest timing decisions must take account for both food abundance and climatic conditions. In many species, photoperiod regulates physical preparations for breeding (Visser *et al.* 2010), however, yearly variation in egg laying dates (Spitzer 1972, Both and Visser 2005), suggests that other, less rigid, external factors may also influence nest timing (Potti 2009, Visser *et al.* 2009, Thorley and Lord 2015). The Bearded Reedling initiates breeding in March, having several broods continuing into August (Cramp and Perrins 1993). Surmacki and Stępniewski (2007) provide evidence of variation in the first egg dates of Bearded Reedlings, with birds laying earlier in years with high spring

temperatures. This flexibility may be vital in multi-brooded species, such as the Bearded Reedling, with earlier breeding times allowing the production of more broods.

Understanding nest site selection processes of bird species can offer insight for conservation, for example, local-scale management can seek to provide or maintain the most preferred habitat characteristics. These may be characteristics that assist the avoidance of predation, with birds known to select components of the habitat that minimise encounters with predators (Lima 2009). Nest site selection should also optimise microclimatic conditions. For example, Lesser Black-Backed Gull, *Larus fuscus*, chicks in areas sheltered from prevailing winds have shown faster growth rates (Kim and Monaghan 2005). Additionally, stochastic events, such as flooding (Robertson and Olsen 2015) should also be considered when selecting nest sites. Several studies have used population level surveys to study breeding distribution of the Bearded Reedling and infer important habitat components (Báldi and Kisbenedek 1999, Poulin *et al.* 2000, 2002, Beemster *et al.* 2010). These indicate that this species is limited to reedbeds, positioning its nests within old stands of reed. However, fine-scale nest site selection is still poorly understood in this species, with most studies being observational (Wawrzyniak and Sohns 1986, Elzen 1993), and one study in Austria (Hoi and Hoi 2001) suggesting nests are positioned in wet, dense reed. With the wide range of this species, variation in structure between reedbeds and differences in management regimes, studies from separate reedbeds may highlight important between-site differences with further relevance to management.

Finally, the structure of the nest itself may have a significant role in the success of a breeding attempt. As separate species show distinct nest structures well suited to providing sufficient support for the developing offspring, nest design was traditionally considered the product of stereotyped, inflexible behaviour (Wallace 1867). However, more recently intraspecific and time dependent variation in nest structure suggests flexibility in nest construction, which may be linked to climatic conditions (Mainwaring *et al.* 2012, Mainwaring, Hartley, *et al.* 2014), predator avoidance (Lima 2009, Biancucci and Martin 2010, Prokop and Trnka 2011, Marasco and Spencer 2015) or experience (Walsh *et al.* 2010, Muth and Healy 2011). In such species, if altering nest design increases breeding success, this plasticity may be a means to buffer against consequences of climatic variation.

Existing local information on Bearded Reedling nest structure from the continent has been summarised in the German language (Wawrzyniak and Sohns 1986, Elzen 1993), but information remains limited from UK populations. As this species is limited only to reedbed habitats nest structure is relatively unique (Wawrzyniak and Sohns 1986), with further information from local sites

potentially offering insight into how this species copes with climatic variation over its extensive range. For example, higher latitude populations, exposed to colder temperatures might be expected to increase the insulating properties of their nests (Hansell 2000).

This study seeks to investigate the timing, nest site selection and nest structure of Bearded Reedlings to better establish the relationship between this scarce species and its specialised habitat. We study one of the most northerly breeding populations of these birds in Europe, at the Tay Reedbeds in Scotland. As this population is at the edge of the Bearded Reedling's geographic range, it offers a useful system in which to study nesting decisions towards the limits in climate that this species can tolerate. Additionally, this site is managed in the form of winter reed cutting to provide heterogeneity in the reed structure for breeding birds. Thus, information on fine-scale nesting decisions can be directly incorporated into future management. We monitor a sample of nests and report the timing of first broods. We then quantify the local nest site characteristics in order to better determine fine-scale nest site selection. Finally, we report measurements of nest dimensions and relate these to local nest site characteristics and climate to establish factors influencing variation in the nest structure of this species.

6.3 Methods and Materials

6.3.1 Study Site

The study was undertaken at the Tay Reedbeds, Scotland (56°23.00'N, -3°10.00'W) in spring 2013, 2014 and 2015. This is the largest continuous stand of common reed on the British Isles, extending for around 4.1km^2. The stretch of the reed in which the nests were located varied in width (distance from the land edge to the river edge), between 200-450m. While the vast majority of the reedbed consisted of dense, uninterrupted stands of reed, in each year small patches of reed were harvested in the winter. These cut patches remained clear of vegetation between January and March, before they were re-occupied by new reed growth which began in April and reached maturity by July. Our study area constituted both, areas with large stands of uncut reed, and areas which included a mosaic of cut patches.

6.3.2 Nest Location and Monitoring

We concentrated on locating nests during the early breeding season, in April and May, as success when nest searching in the later breeding season was limited by dense new growth reducing accessibility of the reed stand (Wawrzyniak and Sohns 1986). Additionally, mature new growth reduced the success of observing breeding individuals, which were often conspicuous at the edges of cut areas when new growth was low. Finally, the distinct call of the Bearded Reedling was used to determine whether birds were present in a given area when there were no clear visual indications; however, this method became ineffective in the later season when adult calls were indistinguishable from fledged juveniles.

The same protocol was undertaken in each year when first locating nest sites. When ringing surveys indicated that birds were in breeding condition (the presence of a brood patch in females or a cloacal protuberance in males), a point transect extending the length of the reedbed was undertaken. This involved visiting vantage points at raised locations along the land edge boundary of the reedbed and provided a general indication to where breeding activity was occurring. Areas of high activity were subsequently visited and potential nest sites identified by watching birds consistently returning to the same areas. Effort was then made to access areas that saw consistent visits. On arrival close to these potential nest sites, birds often emitted alarm calls, indicating the presence of a nest. The nest was then located by searching the area and position recorded using a handheld GPS device. The population was also the subject of an ongoing habitat selection study, which meant that several of the nests located belonged to either colour ringed or radio-tagged

adults. This allowed identification of birds to the individual level and whether a given nest was a second brood of a previously monitored individual.

Upon locating a nest, a record was taken of the finding date, clutch size and age of the chicks (following Svensson 1992). First egg dates were retrospectively calculated by subtracting the age of the chicks, 12 days for incubation (Cramp and Perrins 1993) and an additional number of days equal to the brood size of the given nest, from the finding date. When nests were located at the egg stage, effort was made to record the hatching date, from which first egg date could be estimated. To avoid the trampling of reed stems and consequential creation of tracks to the nests, they were visited minimally: on initial location, when verifying hatching dates on nests located at the egg stage, and when ringing the chicks. The fate of the nest was recorded as successful if it fledged any young and unsuccessful if it was predated or failed for other reasons such as starvation in the nest. Empty nests that had successfully fledged were distinguishable from predated nests as adults feeding fledged young were often conspicuous around the nesting area at the predicted fledging dates.

Other than potential temporal biases created by concentrating only on early broods, we did not expect this protocol to result in the location of a spatially biased sample of nests. The initial point transect covered the full reedbed, meaning breeding activity was recorded in a range of sites within this reedbed. Further, as nests were located over a range of reed characteristics, these factors are unlikely to have caused bias in detectability.

6.3.3 Quantifying nest site characteristics

After the nest became inactive, the reed characteristics surrounding the nest site were quantified. The height of the nest above the ground was measured to the nearest cm. The mean height of five old, dead reed stems within 1m from the nest indicated old reed height. The mean number of dead stems touching a 1m long stick, inserted horizontally at a height of 1m from the ground in 5 evenly spaced directions around the nest allowed quantification of the density of old dead stems. These methods were also used to measure the height and density of new, live, reed stems after the initiation of new growth. However, when new growth was below 1m in height, the stick was inserted at half of the height of the new stems.

Areas of old dense reed that had begun to lean over were given a rating of 1 to 5, with 5 being the most compacted areas. This rating was termed the degree of reed stagger (here on referred to as “stagger”). Mean leaf litter depth in three directions around the nest was also measured to the nearest 5cm. Finally, the mean percentage of water cover around the nest to the

nearest 10% was calculated from 3 measurements taken using a 0.5 x 0.5m quadrat within a 3m a radius from the nest.

In order to compare nest sites with unoccupied sites, reed characteristics were also measured at random locations that were unoccupied by breeding Bearded Reedlings. The study site consisted of a mosaic of reed types: reed cut in the previous winter, young reed which had been left uncut for between 1 and 5 growing seasons and old, previously uncut reed. Despite searching in all patches of the mosaic, every nest was located in old, previously uncut reed (see results). Thus, the choice of random, unoccupied, locations was limited to areas of this old reed. This allowed a comparison of local reed characteristics between occupied and unoccupied sites of old reed, and inference of the key reed characteristics considered in nest site selection within this reed type. 16 random locations were generated in QGIS (QGIS Development Team 2012) but constrained to be more than 10m from a real nest location. The number of random locations equalled the number of nests located. Measurements at an unoccupied site were taken with a week of measurements taken at a real nest.

6.3.4 Quantifying nest dimensions

Nests were collected and frozen for a minimum of 2 weeks and no longer than 4 weeks, before being dried at room temperature for a further 2 weeks. After this, 6 nest characteristics were measured following Mainwaring *et al.* (2014)(See *Figure 6.1*). The external diameter of the nest was measured as the average of the outer diameter at the widest and narrowest axes. The internal diameter was the average of the internal cup diameter at the widest and thinnest axes. The external nest depth was the distance from the top of the nest to its external base. The internal depth was the distance from the top of the nest to the lowest point in the cup. Wall thickness was measured by inserting a pin through the wall at half of the internal cup depth, then taking the average of four measures at evenly spaced intervals. All nest measurements were recorded in cm to the nearest 0.1cm. Finally, nests were also weighed (grams to the nearest 0.1g) using digital scales. Due to the rarity of the nests, we avoided deconstructing them, and so only an external examination was used to qualitatively describe component materials. On completion, the nests were added to Glasgow University's nest archive (Russell *et al.* 2013).

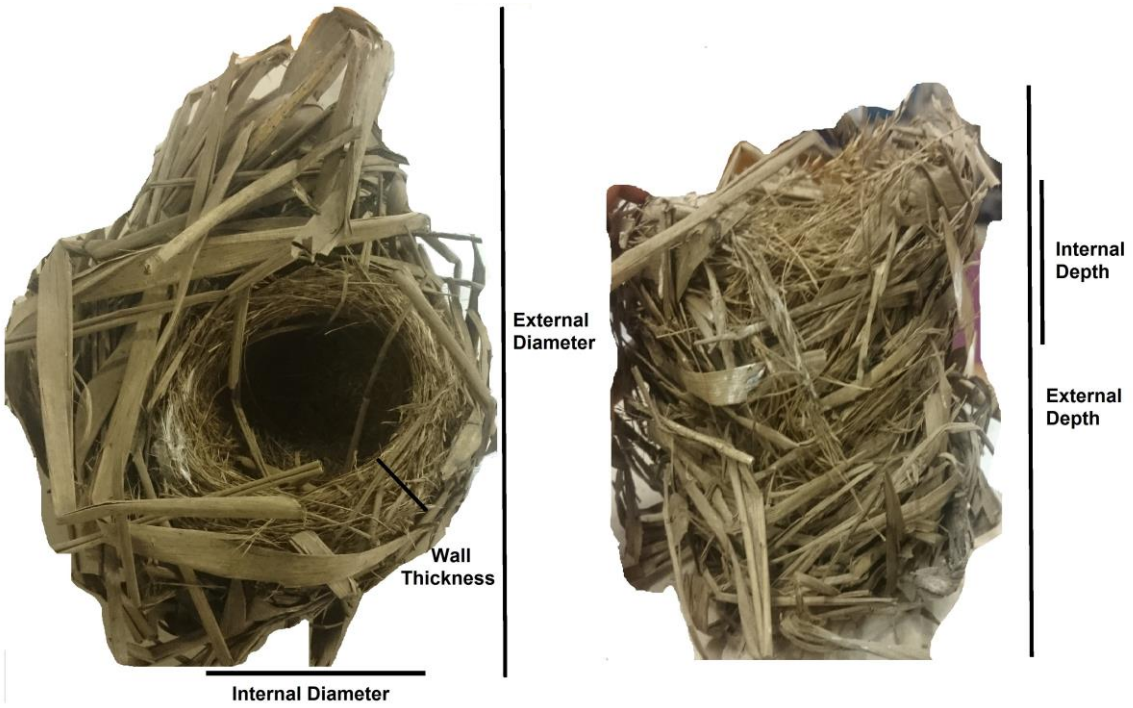

Figure 6.1 – A single Bearded Reedling nest collected from the Tay Reedbeds and recorded nest dimensions. Left panel shows the top of the nest, while the right panel is the view from the side.

6.3.5 Statistical Analysis

The first egg dates, mean average brood sizes and number of nests surviving were calculated for each year and are presented with the mean spring (March-May) temperatures in eastern Scotland for each year (Met Office UK, 2015). Additionally, having exact locations of the nests allowed the distances from the land and river edges of the reedbed to be calculated. The distance from the nearest cut patch was also calculated for nests within 500m of a cut patch. Distances were not included in any of the nest site selection models as sample sizes prevented subsetting of data between managed and unmanaged sites. Similarly, while we obtained too few nests to model the factors influencing nest predation, we provide details of individual nest fates in supplementary material 1.

All data analysis was conducted in R version 3.1.1 (R Development Core Team 2011). Reed characteristics that could predict the probability of a site being occupied by a Bearded Reedling nest were identified using a logistic modelling approach. This involved assigning a binary response to the local nest site data, indicating whether the measurements were taken at an occupied nest site or an unoccupied random location. This binary response was then modelled in a logistic regression with each of the reed characteristics as explanatory variables.

To avoid colinearity in the explanatory variables, prior to modelling, Pearson's correlation coefficients were calculated for each pair of covariates. We avoided the use of principal component analyses due to its potential instability when conducted on datasets with low sample sizes (Guadagnoli and Velicer 1988). Instead, when variables were highly correlated (Pearson's correlation was significant to an alpha level of 0.01), we included only a single variable from the correlated pair in the full model. From each correlated pair, we retained the variable which contributed most to nest site selection. The most parsimonious logistic model was selected using a backwards stepwise selection procedure based on the AIC values of each model. The goodness of fit of the logistic model was tested using the Hosmer and Lemeshow goodness of fit test (Hosmer and Lemeshow 2000) in R package *ResourceSelection* (Lele *et al.* 2014).

We investigated how the dimensions of the nests themselves were related to local nest site characteristics and climatic variables. We first tested how different structural aspects of the nests were associated with each other using Pearson's correlations. We then tested whether these variables could be predicted by the reed characteristics at their given nest site using linear models. Due to small sample sizes, explanatory variables were used to explore each nest attribute individually.

Each nest was assigned a temperature based on the average minimum temperature experienced during nest building. This was estimated as the average daily minimum temperature (data provided by weather underground, 2015, *Ilogfor10* station within 5.5km from the reedbeds, 0m elevation) during the five days prior to first egg date. Here on, this is referred to as the 'building temperature'. Bibby (1983) notes that Bearded Reedlings can continue assembling the nest into the chick stage, and so nest dimensions may more closely correlate with the mean minimum temperature over the period during which the nest was active. Thus, linear models were also run with the mean daily minimum temperature from the first egg date to the last date the nest was seen active. This is subsequently referred to as 'after laying temperature'. Mean minimum temperature was used, rather than overall mean temperature in order to emphasise the variation in the most extreme cold conditions that birds were subject to.

6.4 Results

6.4.1 Nest Timing

In total 16 Bearded Reedling nests were located. 8 were initially located at the egg stage, and 8 as chicks. Almost all were found within the main fieldwork period, with 15 having first egg dates between the 5th of April and the 14th of May. One nest was located outwith this period, with its first egg date on the 21st of June, 2013. *Table 6.1* details the overall first egg dates and brood sizes in each year. No nests were located at the building stages or incomplete clutch stages and so full incubation times were not recorded. Two nests that were located when they contained eggs subsequently fledged successfully, allowing an accurate observation of the time spent in the nest as chicks. This was for 11 and 12 days respectively. Additionally, two of the nests were second broods of birds who's first nests had also been located. In these two cases, the birds had laid the first egg of their subsequent brood 5 and 6 days after their first brood was predated.

Of the 16 nests, 8 (50%) fledged at least one young. This was variable between years (*Table 6.1*). Nest failure was caused by predation at the chick stage in 4 (50%) of the unsuccessful nests. Only one nest (13%) failed at the egg stage, due to egg predation. The remaining 3 (37%) unsuccessful nests were in 2015 when chicks were found dead in the nest at variable ages. Supplementary material 1 provides the reed characteristics and nest fates for each individual nest.

Year	No. Nests Located	First Egg Date	Average Clutch Size (min, max)	% Nests Successful	Mean Spring Temp (°C)
2013	3	13 Apr	6.7 (5,7)	100	6
2014	7	5 Apr	5.8 (5,7)	57	9
2015	6	5 Apr	5.0 (5, 5)	16	7.7

Table 6.1 – First egg dates, clutch sizes and success of Bearded Reedling nests located on the Tay Reedbeds.

6.4.2 Nest Site Selection

All nests were located in mature stands of reed that had not previously been cut. Nests were on average 180m (±16.8 SE) from the land edge and 109m (±13.2m SE) from the river edge. 12 (75%) of the nests were within 500m of a cut patch, with the average distance of these from the nearest cut edge being 29.8m (±4.9m SE). *Table 6.2* summarises the reed characteristics recorded around the nest sites and random, unoccupied sites.

	Mean (SE)	
Reed Characteristic	Occupied	Unoccupied
Old Height (cm)	282.3 (5.4)	254.2(5.55)
Old Density (stems)	26.8 (1.0)	22.1 (1.1)
Degree of Stagger	3.9 (0.2)	2.7 (0.2)
New Height (cm)	61.0 (15.3)	59.3 (17.8)
New Density (stems)	9.8 (1.7)	9.2 (1.4)
Leaf Litter (cm)	26.6 (2.8)	16.9 (1.3)
Water Cover (%)	5.0 (2.0)	11.5 (2.7)

Table 6.2 – Mean and associated SE of reed characteristics at occupied Bearded Reedling nest sites and unoccupied patches of old reed.

Of the habitat characteristics old density and degree of stagger showed a significant positive correlation (Pearson's r = 0.65, P<0.01), as did the height and density of new reed stems (Pearson's r = 0.79, P<0.01). From these pairs of covariates the degree of stagger and density of new stems contributed most to the selection model and were retained. Thus, the full logistic regression model included the height of old reed, degree of stagger, the density of new reed stems, leaf litter depth and the percentage of water cover around the nest. This model suggested that occupied sites had higher stagger ratings and leaf litter depths than unoccupied sites (*Table 6.3; Figure 6.2*).

Covariate	**Δ** AIC	Estimate (SE)	P-Value
Degree of stagger	**0**	**1.71 (0.81)**	**0.03**
Leaf litter (cm)	**0**	**0.16 (0.08)**	**0.04**
Water cover (%)	**0**	**-0.09 (0.05)**	**0.15**
Old height (cm)	1.38	0.03 (0.03)	0.23
New density (stems)	1.58	-0.08 (0.09)	0.5

Table 6.3 – Estimates and associated SE of reed characteristics included in the nest site selection models. ΔAIC values represent the difference in AIC values between the given model and the most supported model. P-Values are calculated from Wald Statistics

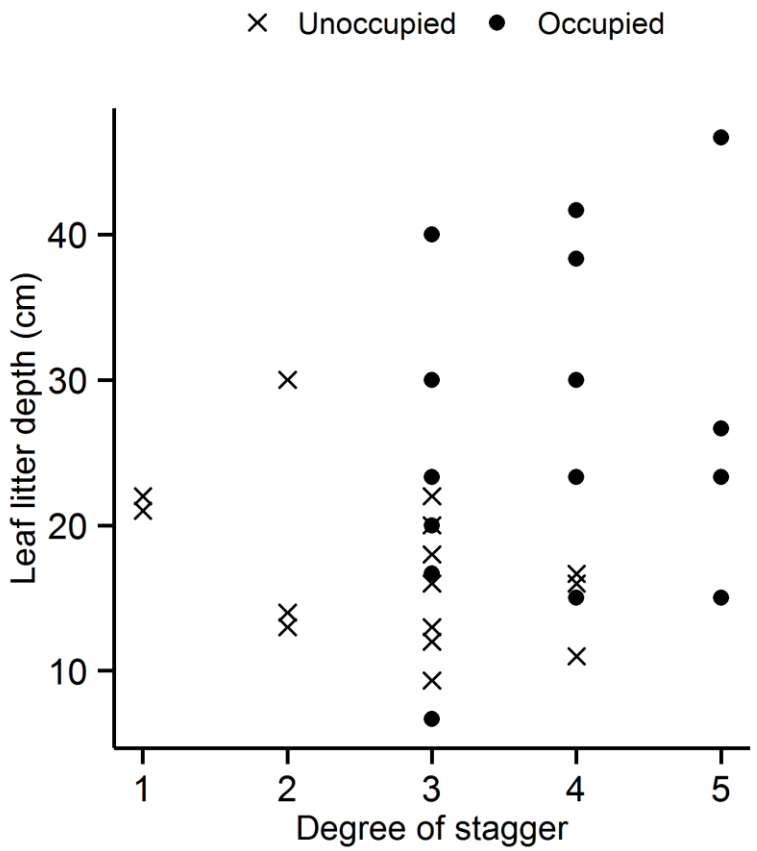

Figure 6.2 – Leaf litter depths and the degree of reed stagger from raw data in occupied Bearded Reedling nest sites and unoccupied patches of mature reed. Residual deviance of most supported model: 22.8 on 28 degrees of freedom; Hosmer and Lemeshow Chi-Squared$_5$ = 8.2, P=0.15.

6.4.3 Nest Dimensions

Measurements of the nest dimensions were taken for only 15 of the nests, as one nest was excluded due to damage sustained from a predation event and subsequent rain prior to its collection. All of the nests were exclusively constructed from *Phragmites,* with different features of the reed being used to build different layser of the nest (See *Figure 6.1* in methods). *Phragmites* leaves formed the main bulk of the structure, being woven to form a thick cone shaped base. Broken *Phragmites* stems of differing sizes provided the main structure for the cup which was thickly lined with soft *Phragmites* seed panicles. This pattern of construction was common to all of the nests located, with all three components being present and occupying the same function in each nest. No nests included additional components, such as other vegetation.

However, the size and quantity of the components differed between nests, resulting in considerable variation in the nest dimensions (*Table 6.4*). Nests with deep external depths tended to have deep internal depths (Pearson's r = 0.59, P=0.026). The deepest nests were also the heaviest (Internal depth: Pearson's r = 0.71, P=0.003; External depth: Pearson's r = 0.57; P=0.023). There was a slight negative relationship between the thickness of the wall and internal nest diameter but this was not significant (Pearson's r = -0.43, P=0.11). There was no relationship between the brood size of the nest and the internal depth (Pearson's r=0.01, P=0.94), internal diameter (Pearson's r=-0.28, P=0.31) or any other nest dimensions.

Nest Dimension	Mean (SE)	Min	Max
Height above Ground (cm)	32.8 (4.21)	6	69
External Diameter (cm)	12.2 (0.14)	9.0	14.5
Internal Diameter (cm)	6.0 (0.21)	4.7	8
External Depth (cm)	9.7 (0.71)	6.3	16.1
Internal Depth (cm)	5.0 (0.19)	3.2	6.1
Wall Thickness (cm)	1.9 (0.12)	1.0	2.8
Weight (g)	29.7 (4.1)	14.8	61.4

Table 6.4 – Nest dimensions, showing: mean, associated standard error, maximum and minimum dimensions of 15 Bearded Reedling nests collected at the Tay Reedbeds.

Nests located in areas of high reed density and stagger showed dense, deep cone shaped bases. This was because nests in these areas were often built into tight gaps within the staggered reeds, becoming misshapen and requiring thick, compacted external depths to remain stable (*lm*; *external depth and density of old stems* $F_{1, 13}=19.55$, $P < 0.001$; *lm; external depth and stagger* $F_{1, 13}=8.42$, $P=0.012$). The internal depth showed a similar relationship to the density of old reeds ($F_{1, 13}=8.15$, $P=0.014$). Smaller nests (with a thinner external diameter) were located in areas with a higher density ($F_{1, 13}=11.62$, $P = 0.005$) and height of new reed growth ($F_{1, 13}=16.45$, $P = 0.001$).

Nests had larger external diameters if they were exposed to lower average minimum temperature both during building (lm: $F_{1, 13}=8.81$, P=0.01) and after laying (lm: $F_{1, 13}=4.35$, P=0.05) (*Figure 6.3*). Wall thicknesses was unaffected by the average minimum temperature during building (lm: $F_{1, 13}=1.18$, P=0.20). However, wall thickness (lm: $F_{1, 13}=4.35$, P=0.05) showed a negative relationship with the average minimum temperature after laying (first egg date to last date seen active). One individual bird had two of its nests located, and another had three of its nests located during the study. These individuals showed distinct variation in external diameter of their located nests, with larger diameters at lower building and after laying temperatures (*Figure 6.3*).

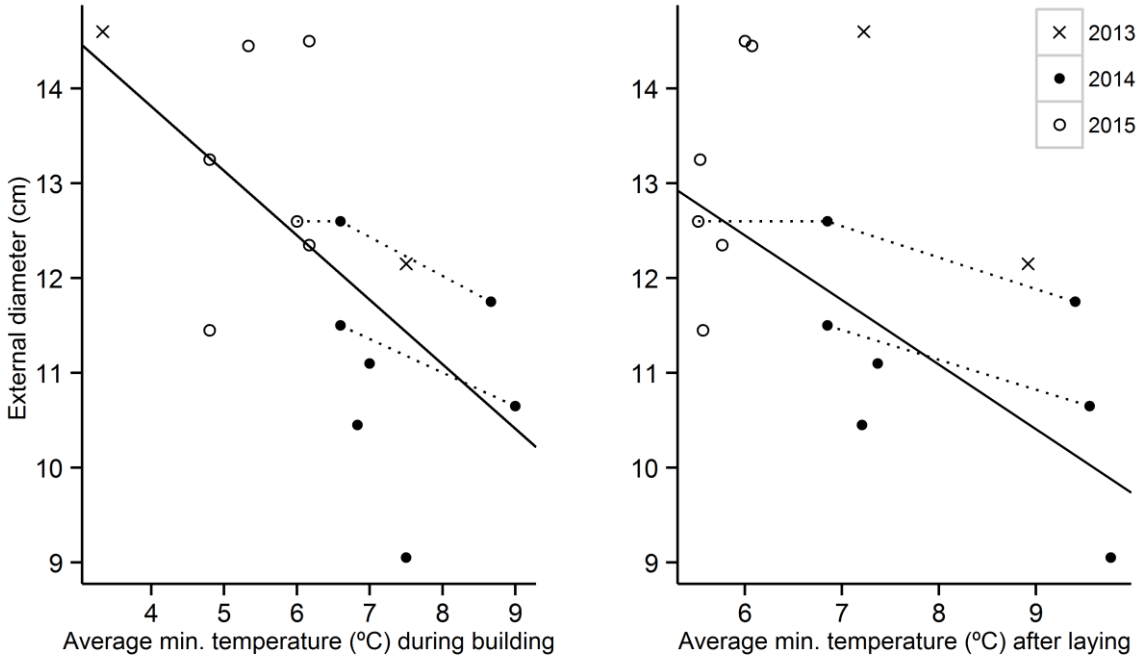

Figure 6.3 – Size of the external diameter of Bearded Reedling nests from the Tay Reedbeds, and the average minimum temperature over the building period (period five days prior to first egg date) and after egg laying. Solid line represents the overall regression. Dotted lines are drawn between nests build by the same individual.

6.5 Discussion

This study provides new information on the Bearded Reedling in respect to the timing of breeding, the general features and specific character of the preferred nest site, the structure of the nest and the flexibility shown in nest construction. Despite a relatively small sample size these factors could have reaching implications for the management and conservation of this reed-dwelling specialist.

Bearded Reedlings on the Tay began nesting at the start of April. Lower latitude populations tend to begin breeding slightly earlier than this, with Wilson (personal communication) reporting that 30% of first egg dates in a long term study at Leighton Moss reedbed in northern England, occurred in March (also see Bibby 1983, Cramp and Perrins 1993, Darolová *et al.* 2008). Beemster *et al.* (2010), demonstrate high peaks of fledged birds occurring in synchrony with the emergence of Chironomids, which are a significant component of the diet of Bearded Reedlings (Bibby 1981, Beemster *et al.* 2010). Thus, synchronisation with prey abundance looks to be an important component of nest timing decisions, and possibly drives the slightly later breeding times of higher latitude birds on the Tay. However, Bibby (1983) notes that earlier breeding times are apparent in eutrophic lakes, while tidal reedbeds are later, so it is unclear if these delays are related to the high latitude of this site.

Surmacki and Stępniewski (2007) show earlier first egg dates at higher spring temperatures in Poland. In our study first egg dates remained consistent despite changes in spring weather conditions. Additionally, we saw rapid relaying times in individuals that had more than one nest monitored, suggesting a pressure to complete multiple breeding attempts in the available season. In multi-brooded species, earlier initiation allows more subsequent broods, causing a trade-off between beginning early and breeding at the most optimal conditions (Crick *et al.* 1993, Kosinski 2001). For Bearded Reedlings, a high reproductive output may be a means to cope with the dramatic winter mortality experienced by this species (Wilson and Peach 2006). Longer term data on breeding phenology at the Tay, potentially available through ringing studies (Peach 2000, Hatton 2008), will better illuminate any trends related to climate in this population and further disentangle yearly and latitudinal variation in the timing of breeding.

All nests occurred in old, previously uncut patches of the reedbed. It is unsurprising that reed cut the previous winter saw no nesting attempts, as the birds begin breeding before regrowth provides sufficient structure. In line with previous studies (Hoi 1989, Hoi and Hoi 2001, Beemster *et al.* 2010), we also found no nests in young reed that had remained uncut for between 1-5 growing seasons. Beemster *et al.* (2010), demonstrate Bearded Reedlings show a preference for the oldest

stands when nesting in a mosaic of old reed and young, previously grazed, reed. Additionally, Bearded Reedlings have been observed undertaking long foraging trips of around 500m (Poulin *et al.* 2000, Beemster *et al.* 2010), suggesting nest site selection is not simply a function of proximity to feeding sites. Clearly, patches of old reed have an important role for nesting Bearded Reedlings.

The logistic models suggested the highest chance of occupancy in areas of this old reed that had a high density of stems. Nests were also positioned in dense reed patches in lake Neusiedl, Austria (Hoi and Hoi 2001). Generally, predation rates of passerine nests decline with stem density in reedbeds (Graveland 1997, Honza *et al.* 1998, Báldi and Batáry 2000, Poulin *et al.* 2002). Species such as reed warblers, *Acrocephalus scirpaceus*, are even known to produce larger and heavier eggs when nesting in dense, more protected territories (Darolová *et al.* 2014). Additionally, our study also showed that the degree of reed compaction, or stagger, was positively selected during nesting decisions, with all nests occurring where there was a medium to high level of reed stagger. Few studies have considered the degree of reed compaction when investigating nest site selection or predation rates (although Tarr *et al.* 2004 conduct similar measurements). An artificial nest experiment conducted on the Tay Reedbeds (Malzer and Helm 2015) highlighted the importance of this reed characteristic in reducing nest predation, potentially by increasing overhead cover and limiting avian predation. Wawrzyniak and Sohns (1986) also suggest overhead cover may function to reduce exposure to strong sunlight.

The selection for areas of high leaf litter, may, however, suggest additional factors are taken into account during nest site selection. Previous studies suggest leaf litter has little effect on nest predation in reedbeds (Batáry *et al.* 2004, Trnka and Prokop 2006, Schiegg *et al.* 2007, Malzer and Helm, 2015). A deep leaf litter in reedbeds can normally only develop in areas with infrequent inundation. Thus, this quality may provide an indication to Bearded Reedlings that a given site is unlikely to flood. As most of the monitored nests were positioned near the ground, they may have been especially susceptible to inundation during high tide events at the Tay (also see Wilson 2005, Wilson and Peach 2006) and selection for dry areas that minimise this risk may be adaptive. Contrastingly, Hoi and Hoi (2001) report greater water depths in nesting areas of Bearded Reedlings in the non-tidal lake Neusiedl and suggest that the choice of these areas reduces predation from terrestrial predators. In tidal sites such as the Tay, inundation may be more frequent and less predictable causing birds to select safe, dry sites. This contrast in results suggests that nest site selection in this species varies between sites and may be dependent on site specific pressures.

The nests located on the Tay showed similar dimensions to those reported for continental birds (Wawrzyniak and Sohns 1986, Elzen 1993). For example, the external diameter for birds in the

Czech Republic and Germany ranged from 8-12cm and 7.5-17cm respectively, while Tay nests showed 9-14cm. Similarly, internal depth on the Tay ranged from 3.2-6.1cm while nests from Austria and Germany ranged from 3-4cm and 4-7cm respectively. Our study suggested that the structure of Bearded Reedling nests on the Tay varied in relation to local nest site characteristics and temperature. As the density of old reeds and degree of stagger increased, nests were larger, with deeper external and internal depths. This variation looked to be driven by the need to build a nest with a robust structure. Nests in sites with high stagger were built up against the reed and often compacted to fit within gaps, whereas nests in less dense areas were positioned directly in the leaf litter with shallow foundations. These results suggest Bearded Reedlings can alter their nests to suit local habitat structure, allowing them to exploit a variety of potential nest sites within old reed stands (see also Wawrzyniak and Sohns 1986).

The relationship of both external diameter and wall thickness with temperature, also suggested nest structure had a role in maintaining optimal microclimatic conditions. Several bird species have shown changes in the insulatory properties of their nests with decreasing temperatures (Hansell 2000, Crossman *et al.* 2011, Mainwaring *et al.* 2012, Mainwaring, Deeming, *et al.* 2014, Mainwaring, Hartley, *et al.* 2014). For example, Mainwaring *et al.* (2014a) show that Blackbirds, *Turdus merula,* in cooler, more northerly parts of the British Isles had larger external diameters. We found, similarly, that Bearded Reedling nests exposed to lower temperatures when building had wider external diameters. Further, we saw thicker walls at higher temperatures when temperatures after laying were considered. The birds potentially construct larger nests when exposed to lower temperatures during building, and as temperatures change during the active nest stages, the wall size is altered. This is in line with previous studies which suggest alteration of the nest structure can continue into the active incubation and chick phases (Wawrzyniak and Sohns 1986). This effect was consistent in individuals that had several broods, suggesting that this flexibility is maintained between broods. The clarity in these results may be driven by the confinement of this species to few nesting materials, removing potentially confounding variation in the availability of nesting materials.

The conclusions of this study can be used to inform the future conservation management of reedbed habitats. Many reedbeds are subject to cutting, grazing or flooding management to reset succession and increase reed vigour. While these practices can provide effective foraging sites for reed specialists including the Bearded Reedling (Valkama *et al.* 2008, Beemster *et al.* 2010), our results clearly suggest that effective management should also ensure adequate areas of old reed is available as nesting habitat. As we found no nests in areas of reed uncut for less than five years, when designating areas for nesting habitat, management should be excluded over the long term to

allow adequate leaf litter and reed compaction to form. Indeed, where flexible hydrological control is possible, drawdown of water levels during the breeding season may provide further nesting habitat, offering drier areas of leaf litter. While this prescription may benefit the Bearded Reedling, management should also consider the requirements of other protected reedbed species. Bitterns, *Botaurus stellaris,* require water depths of between 10 and 97cm before nesting (Gilbert *et al.* 2005, Polak 2007), while reed warblers may benefit from the presence of non-reed vegetation (Darolová *et al.* 2014). An effective strategy that is likely to offer resources for a range of species is that of a dynamic habitat mosaic where areas of old reed, early successional stages and open water can occur in parallel.

Our results also provide relevant information for the wider conservation of the Bearded Reedling. The ability of Bearded Reedlings to flexibly produce multiple broods, could assist this species when coping with both inter-annual and long term climatic variation. Similarly, being able to alter nest structure in relation to local temperature may provide a means to buffer against environmental change. In understanding the factors governing fine-scale nesting decisions, conservationists can develop well informed management strategies which may prove critical for the protection of rare and specialist species.

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Chapter Seven

Proceedings of a symposium concerning the status of the Bearded Reedling, *Panurus biarmicus,* in the UK

Iain Malzer, Rodney West

7.1 Abstract

In February 2015, Stanny Field Centre at Stanny House Farm, Suffolk, hosted a small symposium concerning the current status, monitoring methods and implications of reedbed management for the Bearded Reedling, *Panurus biarmicus*, in the UK. The following overview presents some aspects of this discussion and highlights the need for across site collaboration and communication.

7.2 Introduction

The Bearded Reedling, or Bearded Tit, *Panurus biarmicus*, is a reedbed dwelling Passerine. An extensive range throughout Eurasia has led the IUCN to categorise this species as 'of least concern'. However, specialisation to reedbed habitats drives a localised and fragmented population structure at a wide-scale. In the UK this localisation earns the Bearded Reedling a place on the Amber list for birds of conservation concern (Eaton *et al.* 2009). This constraint to sufficient reed habitats also limits any conservation efforts to a finite number of sites throughout the UK, emphasising the importance of adequate monitoring and management at these sites. In February, 2015, a small symposium concerning the current status of the Bearded Reedling in the UK was hosted by Stanny Field Centre, Stanny House Farm in Suffolk. Here, delegates highlighted the most important current threats to this species. They then introduced appropriate monitoring methods at several sites of importance to this species throughout the British Isles. Finally, an array of different reedbed management strategies, and their implications for Bearded Reedlings were discussed. The following draws attention to some important aspects of the symposium's discussion, while making suggestions for the future conservation of this unique species.

7.3 Present and Future Threats

The most important threat to Bearded Reedlings is habitat loss. Reedbed is one of the rarest habitats in the UK (Hawke and Jose 1996). It is an intermediate stage of succession between aquatic vegetation and scrubland. Thus, by nature this habitat is temporal. Drainage schemes and water extraction have meant a reduction in the formation of new reedbeds to replace sites which have dried out (Bibby and Lunn 1982, Everett 1989). Thus, currently much effort is placed into the preservation of current protected reedbed sites, the majority of which are on the south-east English coast. However, many of these sites are faced with an imminent threat from coastal inundation (IPCC 2007). The creation of new reedbeds, especially inland freshwater sites, may be the most effective way to combat the threats to reed specialists of habitat loss. Projects, such as the National Trust's '100 year vision for Wicken Fen', where they will eventually create around 56km^2 of wetland, will be vital for the long term stability of these species.

Climatic change may also have more direct consequences for Bearded Reedlings. Global change models suggest an increase in the frequency of extreme weather events, such as flooding (IPCC 2007). These can block access to the reedbed's leaf litter layer, the main winter foraging site for Bearded Reedlings, potentially resulting in high winter mortality (Wilson and Peach 2006). The vulnerability of the Bearded Reedling to adverse winter conditions has been a reason for major

population fluctuations demonstrated at many of the sites discussed (also see van Turnhout *et al.* 2010). Records from Walberswick have shown fluctuations between 10 and 100 breeding pairs in the space of a few years. Similarly, large crashes have been recorded at the Tay (*Figure 7.1*), Leighton Moss and Minsmere. Recoveries can be rapid as this species can begin breeding in March, and, when conditions permit, have several broods throughout the season until August (Cramp and Perrins 1993). A series of extreme winters, however, may limit this recovery and offer a serious threat to Bearded Reedling populations.

Many species show elevated breeding ranges as northern latitudes become milder (Newton 2008). The range of the Bearded Reedling is severely limited by the availability of reedbed habitat and so its ability to exploit more northerly latitudes will be more restricted than other species. However, interestingly, the discussion highlighted that in many of the longest studied Bearded Reedling populations, the number of wide-scale ringing controls has decreased dramatically between the 1970s and 1990s, so that UK birds would now appear to be less mobile than previously. If the occasional wide movements of this species are driven by harsh winters or other climatic factors (Surmacki and Stępniewski 2003; Surmacki and Stępniewski 2007), the perceived idleness of Bearded Reedling populations over the last two decades could be indicative of a recent temporal reduction in these pressures.

7.4 Monitoring Methods for Bearded Reedlings

Clearly, many of the threats to the Bearded Reedling are at a wide-scale, with changes likely to be gradual and long term. Recognising changes in patterns of distribution and abundance will be essential when aiming to mitigate current threats. This will only be achievable if adequate species monitoring methods are in place at key sites. Thus, much of the discussion concerned the most appropriate ways in which to monitor these birds at a local-scale.

Currently, the rare breeding birds panel (RBBP) offer the most useful yearly estimates of Bearded Reedlings in the UK. An average estimate of 527 breeding pairs has been suggested for the five years including and previous to 2012 (Holling and RBBP 2012). These estimates are collated from counts at around 60 sites throughout the UK and their accuracy is dependent on the submission of counts from key breeding sites. The discussion, however, highlighted how problems of limited accessibility and the timing of counts could have a strong influence on relative yearly comparisons.

In the UK, there are around 60km^2 of reedbed. The vast majority of these reed stands are less than 0.2km^2 in area and can vary dramatically in size and structure (Hawke and Jose 1996). This structural variation drives the first major difficulty in designing consistent and effective monitoring methods for this species. Changing accessibility to reedbeds means that several sites will not have adequate spatial coverage during sampling. Traditional sampling normally involves point count or transect methods that may be especially successful in small reedbeds and when observations can be made from elevated positions (Surmacki and Stępniewski 2003; Poulin *et al*. 2000). In some cases these methods may still be appropriate for larger reedbeds (Beemster *et al.* 2010). For example, at Minsmere and Walberswick pathways, raised bunds and bird hides allow a network of accessible points throughout the reedbed. These are visited several times throughout the breeding season allowing the identification of breeding pairs and general nesting sites. In addition, on the Norfolk Broads and at Easton in Suffolk carefully timed counts from a punt or canoe of newly fledged first broods as they emerge onto the edges of meres or canals has proved a useful means of assessment. However, such systems are not always feasible, and in many of the largest sites, which intuitively hold the largest populations of these birds, spatial coverage is limited.

While spatial coverage is a major difficultly when monitoring these birds, several sites highlighted the additional importance of subtle temporal changes when conducting surveys. The detectability of Bearded Reedlings can vary considerably throughout the breeding season. When incubating eggs, the birds are often elusive, nesting close to the ground in dense areas of reed. Thus, surveys that coincide with the incubation period in a given year result in far fewer contacts with birds than surveys conducted during chick provisioning. Surveys mistimed by only a few days could severely underestimate numbers and invalidate comparisons between years. This problem is further accentuated by the tendency of Bearded Reedlings to begin breeding early, making them susceptible to prolonged winters and causing considerable yearly variation in first laying dates. A high effort survey design, where observations are repeated several times throughout the season could mitigate these problems. However, combining surveys with information regarding breeding condition, collected during bird ringing, is preferable where possible.

Figure 7.1 Mist nets erected in a relatively accessible area of the Tay Reedbeds.

Bird ringing techniques are possibly the most effective methods with which to survey Bearded Reedlings in large reedbeds (Peach 2000, Poulin *et al.* 2000). Problems of accessibility may be overcome by positioning nets in only the most accessible areas of the reedbed (*Figure 7.1*). Temporal changes in detectability are unlikely to have as important an effect as netting sessions can last around six hours, during which even incubating birds are likely to move several times. In addition, tape lures can be used to encourage birds into the nets. At their simplest, when consistent, bird ringing methods allow annual totals of ringed birds to be compared between years (*Figure 7.2*). However, levels of analytical complexity may be added, with population sizes and survival rates being estimable using capture recapture methods. These methods have been valuable in large reedbeds such as the Tay where members of the Tay Ringing Group input commendable effort to catch Bearded Reedlings throughout the breeding season (Peach 2000, Hatton 2008), ringing 764 new individuals throughout 2014.

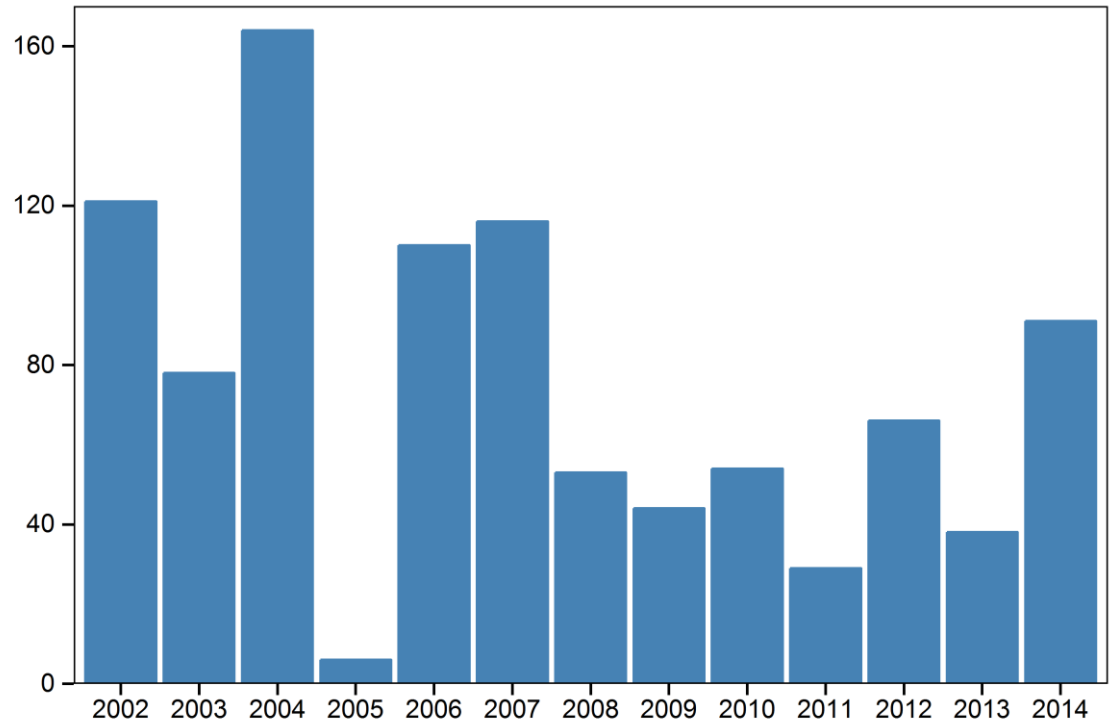

Figure 7.2. The numbers of unique adult Bearded Reedlings caught by the Tay Ringing Group during consistent breeding season ringing sessions at the Tay Reedbeds.

Further to this, ringing data can offer more detailed information on breeding condition, demography, moult and individual movements (*Figure 7.3*). Ringers also have an intricate knowledge of their study species, noticing and detailing variation in morphological characteristics that can result in wide reaching conclusions. For example the beard length of Bearded Reedlings is reported as being a condition dependent trait on which females base their mate choice (Hoi and Griggio 2008). Further subtle changes in the eye colour of juveniles can allow prediction of fledging dates (Pearson 1975, Wilson and Hartley 2007) or, potentially, inference of population origins (Pearson 1966). With normally less than 1000 Bearded Reedlings being ringed each year in the UK, forums which highlight such ringing research and facilitate wider-scale collection of less traditional biometric measurements could be of high value.

Leighton Moss, an RSPB reserve in Lancashire, uses several of these monitoring methods in a successful long term strategy. This is the largest reedbed in northern England at an area of around 0.79km^2 and can have up to 65 breeding pairs of Bearded Reedlings (Wilson 1993). Year round ringing is consistent in several sites throughout the reedbed during which each individual is given a unique colour ring combination allowing their subsequent identification without capture. Resighting individuals during the breeding season is then assisted by the tendency of the birds to nest in

artificial nest boxes constructed from reed (Wilson 2005). During the winter, further resightings are made at grit provisioning sites (Wilson 2014). This consistency in monitoring has allowed the identification of key factors which may limit the population success of Bearded Reedlings at Leighton Moss, such as persistent winter flooding (Wilson and Peach 2006). Clearly, sites like this are of vital importance when identifying current threats and successful management methods, many of which will be applicable for other reed sites. However, only with commendable effort from both volunteers and professionals is the maintenance of this consistency achievable.

Figure 7.3. A male Bearded Reedling in a mist net, captured during May 2014 on the Tay Reedbeds.

The discussion concluded that there is no single answer for the wide-scale monitoring of this species. Monitoring methods are unique to individual sites. Thus, overall estimates which collate information from several different monitoring methods, such as those used by the RBBP, may be the most adequate. However, since monitoring accuracy will likely decrease in proportion to the size of the reedbed, these methods should account for differing accuracies between sites. In addition, wider-scale estimates should not overlook the importance of small reedbed fragments to Bearded Reedlings. These areas are likely to be occupied only sporadically by relatively few breeding pairs. However, with the majority of British reedbeds being limited in size, birds at small sites could form a significant proportion of the overall population. A widescale effort from the general birding community to consistently check local reedbed sites for Bearded Reedlings would provide invaluable insight into the changing distributions of these birds, how this relates to abundance at key sites and major population trends. Such information when communicated consistently could readily be incorporated into, and enhance, the accuracy of RBBP estimates.

7.5 Reedbed Management

As well as indicating long term trends, adequate monitoring methods will provide insight into the implications of reedbed management for the Bearded Reedling. Two main motives exist for reedbed management. The first is to maintain the long term integrity of the reedbed by impeding succession. The second involves the encouragement of structural heterogeneity throughout the reedbed, which offers species the chance to exploit different patches of resources. Again, management methods are site specific, with practices varying with the size and structure of reedbeds. Reedbed management is normally undertaken in two ways; the control of water levels and the direct cutting of the reed itself (Bibby and Lunn 1982, Hawke and Jose 1996). Both methods may have wide consequences for a variety of species.

The discussion highlighted some potential consequences for the Bearded Reedling by comparing and identifying important aspects of the local habitat between different sites and how these change with management. Despite the discussed reedbed sites covering a wide variety of structures, from large tidal estuary reedbeds to narrow, linear reedbed strips which follow water courses, persistent patterns in habitat use emerged. Bearded Reedlings consistently showed a preference for nesting within dry areas of the reedbed with high levels of leaf litter. For example, in a small reedbed at Farlington Marshes in Hampshire, breeding Bearded Reedlings shifted their nesting sites between years to the driest areas of the reedbed as the distribution of water changed. This preference has been noted before (Bibby 1981, Bibby and Lunn 1982, Beemster *et al.* 2010). These dry areas are normally old, mature, unmanaged patches of reed and provide thick, often staggered reed stems to act as nest foundations (Hoi 1989). These dense and impenetrable areas presumably offer effective protection from predation (Báldi and Batáry 2000, Batáry *et al.* 2004).

Observations of Bearded Reedlings have shown distant parental foraging flights of as far as 500 metres in reedbeds throughout Europe (Poulin *et al.* 2000, Beemster *et al.* 2010). In breeding surveys conducted in the UK sites discussed, summer foraging was consistently in wet areas of the reedbed. These areas offer high invertebrate abundance, with Bearded Reedlings exploiting hatches at the edges of small pools (Bibby and Lunn 1982, Hawke and Jose 1996). Thus, at its simplest, management that maintains both old reed patches and wet areas should facilitate breeding Bearded Reedling populations. However, Beemster *et al.* (2010) demonstrate the importance of early stages of reed growth created by grazing herbivores for foraging Bearded Reedlings and suggest visual foraging cues are more obvious in these patches. Winter reed cutting can simulate reed growth in a

similar manner, removing blocks of reed which will begin to grow back over spring (*Figure 7.4*). Valkama *et al.* (2008) demonstrate the tendency of cut sites to grow back more densely, to a lower height with a thinner diameter and lower leaf litter than old, uncut patches. Again, this lower complexity at cut sites may assist accessibility offering effective foraging patches (Trnka *et al.* 2009, Beemster *et al.* 2010).

Figure 7.4 - A block of reed cut in January 2014 on the Tay Reedbed. Photographed here in May 2014 as new growth initiates.

The effects of this management on invertebrate abundance are, however, less clear. While several studies have found increases in abundance in cut patches (Beemster *et al*. 2010; Poulin and Lefebvre 2002), a meta-analysis by Valkama *et al* (2008) suggests effects are variable between sites, management methods and invertebrate species. Recently, studies have shown more consistently increased invertebrate abundances measured in reedbeds cut in a mosaic pattern (Poulin and Lefebvre 2002, Schmidt *et al.* 2005, Beemster *et al.* 2010, Trnka *et al.* 2014). As most managed UK sites are cut to assist conservation rather than for commercial reasons, here, most reed management plans already aim to achieve a mosaic pattern with high heterogeneity in the structure of the reedbed.

While there seems to be general agreement that stimulation of reedbed heterogeneity will benefit foraging Bearded Reedlings, reed cutting could have adverse consequences from other biological perspectives. For example, researchers at the Tay have been observing how the predation rates of artificial nests at the edges of cut areas change throughout the breeding season, with artificial nests in the early season being most heavily predated. The accessibility of the cut areas in the early season, prior to the initiation of new growth, could drive these increased predation pressures (Trnka *et al.* 2014). In addition, the Bearded Reedling changes its diet from insects to reed seed in the winter. It is therefore likely to have different requirements during this seasonal phase than in the breeding season. Higher reed seed indexes have been reported in new growth at recently grazed sites (Beemster *et al.* 2010). However, these are based on seed panicles which are a less important winter foraging resource than a deep, seed filled, leaf litter for Bearded Reedlings (Wawrzyniak and Sohns 1986), an observation shared between many attending the discussion. Finally, the importance of smaller, more fragmented reedbed sites may have an important role during the winter (Surmacki and Stępniewski 2003) and should be considered in management.

7.6 Outcome

The dependency of the Bearded Reedling on restricted reedbed habitats means extra effort is needed to properly monitor these birds. Species specific forums and discussions between individuals working at relevant sites are essential in allowing the communication and exchange of current techniques and trends. Such collaboration may be especially important in highlighting the major threats to the Bearded Reedling, which look to be gradual and long term. Despite this, the meeting emphasized the variation in reedbed size and structure throughout the UK, concluding that a single monitoring method to suit all sites is unfeasible. Future questions regarding the overall status of this species in the UK should incorporate and draw from several different monitoring methods. While appropriate reed management strategies are also highly site specific, general ground observations about habitat preference were conserved between sites and congruent with any literature discussed. In the UK, reedbed management looks to be moving in a direction compatible with the requirements of the Bearded Reedling, at least in providing heterogeneity throughout the reedbed. However, information about the direct nesting biology and the changing seasonal requirements of this species is needed to complete the picture. Questions which will be greatly assisted by further cross site comparisons and collaboration.

7.7 The Way Forward

A push for public and wide-scale collaboration could actively assist the plight of the Bearded Reedling in the UK. A forum, to discuss the Bearded Reedling has been set up at **www.groups.yahoo.com/group/reedling**, to subscribe to the mailing list and keep up to date send a blank email to **reedling-subscribe@yahoogroups.com**. This initial step will allow the between site communication discussed and offer an environment in which bird ringers can standardise and compare data collection methods. Another main function for this site is to allow interested members of the wider birding community to become more officially involved, contributing observations and insight. If birdwatchers can consistently check small, local reedbed sites for these birds and contribute this information, they could supplement data collated by the RBBP and assist in the production of accurate abundance and distribution estimates. Together we can then aim to make the Bearded Reedling less enigmatic and assemble quality data regarding population trends and movements that will allow more informed and decisive long term conservation efforts.

7.8 Acknowledgements

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Chapter Eight

The movement patterns of a specialist resident, the Bearded Reedling, *Panurus biarmicus.*

Iain Malzer, Barbara Helm

8.1 Abstract

To avoid the most unfavourable conditions in a seasonally changing environment many bird species migrate. However, species that are highly specialised to specific habitats can benefit from remaining locally. Distinct adaptations for year-around residency may limit the capacity for long distance movement during migration and possibly dispersal. Because movement patterns of specialist resident species need better refined we study the wider movements of the Bearded Reedling, *Panurus biarmicus*. This reedbed specialist has short wings and undergoes distinct seasonal changes in gut structure, making it well adapted to residency. Using ringing recoveries provided by EURING, we investigate the Bearded Reedling's movement patterns in different regions of Europe. We use summer to summer recoveries to establish patterns of dispersal. We then explore distance and direction of recoveries throughout the year to determine the importance of migratory movements. We find a range of movement strategies. Birds breeding in southern Europe remained sedentary, and only occasionally undertook long distance movements during dispersal. UK birds showed directed, longitudinal migration, exploiting more reedbed sites during the winter. Birds from east, west and north Europe showed marked latitudinal movements, resembling classical partial short distance migration. In all regions some individuals were recorded at all times of year near breeding grounds. Dispersal distances were high for all regions, and neither migratory nor dispersive movements differed between the sexes and age groups. Despite being adapted to remaining resident, this species has retained the capacity to undertake wider movements, and in areas with marked seasonality these movements can approach regular migration.

> *"The Bearded Tit has never been reported from any of the Norfolk light-stations, but a single bird seems to have occurred at the Languard Light, Suffolk, on the 16th of Febuary, 1987. A note quoted in the same Report from a Yarmouth correspondent, who is unnamed, stating that on the 18th of November a 'nice lot of Bearded Tits are said to have come in from a great height and from the E.' lacks any corroborative evidence, and from its improbability cannot, I think, be accepted."*
>
> *B. B. Riviere, 1930, "A history of the birds of Norfolk"*

8.2 Introduction

Most global environments show a degree of annual change to which organisms must find ways to adjust. The high mobility of birds provides them with the option to undertake wide movements, allowing many species to avoid periods of unfavourable conditions by migrating (Newton 2008, 2011). However, some species remain and endure even in the face of substantial seasonal changes in their local environment. These behaviours may be seen as extremes on opposite ends of a continuum, with specialised programmes for long-distance migrations on the one end and adaptations in behaviour and physiology allowing local residency on the other. Between these extremes lies a broad range of variation between migratory species, and even single species can occupy an array of positions on this continuum (Korpimäki 1986, Berthold *et al.* 1992, Helm *et al.* 2006).

Variations in movements are commonly classified along one or more axes: a main axis arranges migration strategies mainly by distance of travel. Several features are thought to commonly align with increasing migration distance, although they can also vary independently (Newton 2011). These include morphology and physiology, for example increasing wing pointedness with increasing distance (Winkler and Leisler 1992, Senar *et al.* 1994, Baldwin *et al.* 2010), but also patterns of movement such as, increasing spatio-temporal consistency of movements within a species, a local population, and an individual across its life-span (Newton 2011). Thus, at the extreme migrant end of the scale, on a population level, all members of a population are expected to be migrants, showing clear, seasonally correct, directionality, distance and synchrony of movements. At an individual level, this corresponds to consistent migratory features over the lifespan of an individual (obligate migration). While these features are well integrated on the migrant end of the gradient, where the prevailing mode of regulation is obligate migration (Alerstam *et al.* 2003), they are much less clear for the resident end. The resident end could be characterised either by similarly consistent behaviour (obligate sedentariness), or, conversely, by maximal flexibility (facultative migration).

To better understand movement strategies on the resident side of the spectrum, species which show strong adaptations to remaining resident may enable valuable insights. Adaptations may be seasonal changes such as winter fattening (Blem 1976, Gosler 2011), territoriality (Cuadrado 1997) or food caching (Pravosudov and Grubb 1990), which allow individuals to remain in their breeding ranges year round. Such species may, nonetheless, undertake occasional wider-scale movements. For example, partial migrant populations contain both resident and migratory individuals (Terrill and Able 1988). Other normally resident species can demonstrate large-scale,

irregular movements during irruptions related to environmental conditions (Newton 2006, 2011, Lindén *et al.* 2011). For these species, the benefits of departing under difficult conditions will need to be carefully balanced against lost local opportunities, and may conflict with adaptations for overwintering locally.

In addition to such graded seasonal migrations, occasional wider-scale movements of predominantly resident species may occur during dispersal. Dispersal is defined as the movements between breeding sites for adults, and movements between natal and breeding sites for juveniles (Greenwood and Harvey 1982). In many species, dispersal differs between the sexes and age groups, and dispersive movements tend to be in any direction (Greenwood and Harvey 1982, Newton and Marquiss 1983, Newton 2010). Dispersal distances have been suggested to correlate with migration distances, suggesting shorter movements in resident species (Paradis *et al.* 1998).

To investigate movements on the resident end of a migration gradient, we studied the Bearded Reedling, *Panurus biarmicus*, which is a highly specialist, year-round resident reedbed songbird. It has a wide distribution throughout Eurasia, but is completely localised to patches of *Phragmites* reed on which it depends when sheltering, nesting and foraging. In contrast to other reed specialist Passerines, such as many migratory *Acrocephalus* warblers (Leisler 2011), Bearded Reedlings show clear adaptations that allow them to remain within local, high-latitude reedbeds for the full year. One key adaptation towards residency is a seasonal shift in diet from invertebrates in the summer to almost exclusively reed seed over the winter (Bibby 1981). This shift requires a substantial change in the morphology of the digestive tract (Spitzer 1972). Gizzard mass on average doubles, increasing by 0.5g (ie, by 2-5% of total body mass), and becomes lined by a thick, plated, keratinous layer. This change coincides with the seasonal ingestion of grit, which further adds to body mass (Spitzer 1972, Wilson 2014). These changes, which are reversed in late winter, are maintained in captive birds that have ad libitum access to food year-around, and are timed by photoperiodic change (Spitzer 1972). Further adaptations in morphology, such as the small rounded wing (Peiro *et al.* 2006) and long tail (Romero-Pujante *et al.* 2002, 2005), are well suited to movement within reedbeds, but inefficient during longer distance flights (Winkler and Leisler 1992). This species clearly demonstrates a high propensity to remain as a resident, and to suffer major constraints during migration from both seasonal physiology (Piersma and Gill 1998) and flight apparatus (Winkler and Leisler 1992).

These constraints and the associated strong resident tendency may have population-level consequences for survival on occasions when local conditions become extremely unfavourable. Bearded Reedlings are notorious for wide population fluctuations (Pearson 1975, Bibby 1981, Wilson

and Peach 2006, Surmacki and Stępniewski 2007, Beemster *et al.* 2010), which are partly related to winter mortality. Wilson and Peach (2006) demonstrate that an extreme winter flooding event in a reed stand in northern England reduced a wintering population by over 90%, as the seeds in the litter layer became inaccessible. Similar effects may be important in years with extreme frost and snow. In addition, this species' dependence on a single species monoculture during the winter can put it at risk during years when seed production is low (Bock and Lepthien 1976, Koenig and Knops 2001, Newton 2006). Clearly, in some years this species will encounter intolerable local conditions and movement may be a better option than remaining resident. This may have favoured a readiness to move, despite clear constraints towards residency, at least in parts of the population.

At present, we have no clear understanding of the movements of Bearded Reedlings. Locally, varying movement tendencies have been reported from their wide breeding range, from residency in Spain and Italy (Marin and Marchesini 1994, Peiro 2013), to eruptive migration in Austria (Spitzer 1972) and England (Axell 1966), to seasonal migration in Germany (Dürr *et al.* 1999). A brief summary of these patterns is given by Elzen (1993). These studies are difficult to interpret because they have differed in methodology and have lacked integration on a larger spatial scale. To establish the patterns of movement undertaken by Bearded Reedlings, we therefore performed a wide-scale analysis of the European ringing recoveries, provided in a EURING dataset. Our main goals were:

i) to examine spatial heterogeneity of movements. We addressed this by comparing the recoveries of five geographic areas across Europe, grouped along common migration patterns of songbirds, while allowing relatively balanced group sizes (*Figure 8.1*).

ii) to analyse dispersal in these areas by investigating movements of birds first captured in summer and recaptured in a subsequent summer. Following patterns of dispersal in other songbirds (Newton 2008), we expected higher dispersal distances in birds first caught as juveniles, differences between the sexes, increasing dispersal distances with increasing migration distances, and no indication of preferred direction.

iii) to analyse seasonal movements (spring migration: winter to summer; autumn migration: summer to winter). To more rigorously integrate the movements of Bearded Reedlings into frameworks of a migratory continuum (Newton 2011), we used the mean and spread of distance and directionality of recoveries throughout the annual cycle as descriptors for classifying movement. Proportions of migratory and resident individuals could not be quantified from ringing data as local birds are typically not reported. We expected that if Bearded Reedlings performed classical seasonal

migration, recovery distances should increase with time from summer, peak in winter, and decline again in the following spring (Newton 2011). Additionally, consistent changes in the directions of movements occurring during conventional autumn and spring migratory periods, should further indicate whether there is regularity in the movements, and assist in positioning this species on the migratory continuum.

8.3 Methods and Materials

8.3.1 Datasets

The EURING databank provided 4191 recoveries of 3345 individual Bearded Reedlings that were greater than 5km in distance from their original capture. We retained records of over 5km as movements over this threshold are consistently submitted to the EURING databank by all the contributing ringing schemes (Sauter *et al.* 2010). Hereafter, 'recovery' refers to both live trapped birds and ring numbers reported from dead birds. 43 recoveries of birds that had been hand reared or intentionally moved according to the 'manipulated' and 'moved' variables (du Fue *et al.* 2012) were removed from the dataset. A further 9 birds were removed as their recovery date was less accurate than to within two weeks either side of the recorded date. 99% of recovery locations were accurate to a distance within 5km, and those outwith this remained in the analysis as all were accurate to within 50km. This left 4138 recoveries of 3304 individuals recorded between 1954 and 2011.

We assigned the recoveries into different regions of Europe, based on the region in which the bird was first captured. The regions were defined based on previous studies of this species, and other similar species (See *Figure 8.1*). We split central Europe into eastern and western regions as several species show distinct migratory routes in these regions (Sauter *et al.* 2010, Andueza *et al.* 2014). These regions also distinguish between two Bearded Reedling populations for which previous information concerning local movement patterns is available (Wawrzyniak and Sohns 1986, Elzen 1993, Dürr *et al.* 1999, Hofiák *et al.* 2003). We also examined birds from the British Isles (Pearson 1975, Campbell *et al.* 1992, Cramp and Perrins 1993) and from the most northerly and southerly latitudes, respectively, as these populations may experience distinct climatic profiles (Peiro 2013). The regional pooling occurred over relatively large geographic areas to ensure adequate sample sizes in regions such as the south and north. Pooling over smaller areas would have led to too few recoveries in some areas for effective analysis

We also defined each Bearded Reedling recovery as either a winter or summer recovery. These birds begin breeding in March and may have several broods between March and August (Cramp and Perrins 1993). Adults and juveniles captured in this period are assumed to have been at, or close to, their breeding and natal sites respectively. Only 1% of the movements in the full dataset occurred within the same summer, suggesting the birds remain localised during the breeding season. Recoveries outwith this period were considered winter recoveries.

Finally, the recoveries were further split to produce distinct datasets which should provide insight into the specific patterns of movements; the 'dispersal' dataset, the 'seasonality' dataset and finally the 'migratory period' dataset. All data organisation and analysis was conducted in R Statistical Environment (R Development Core Team 2011).

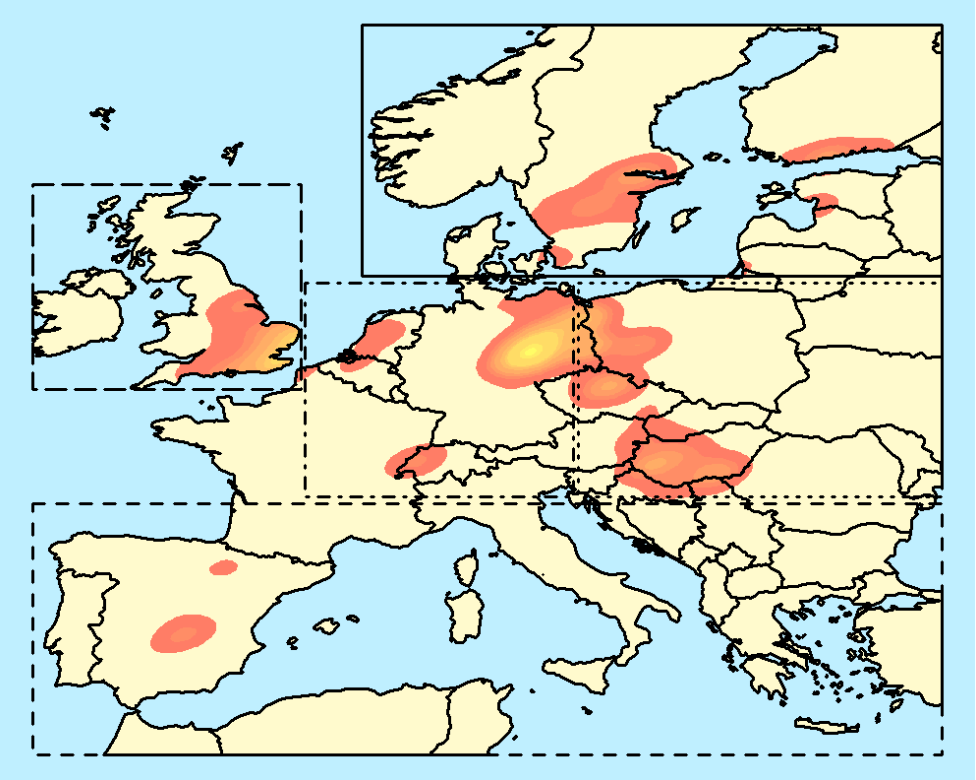

Figure 8.1 – Distribution of 4138 ringing recoveries throughout Europe depicted using a bivarate kernel density smoother. Strongest yellow areas are sites with highest numbers of recoveries. Boxes represent regions between which the dataset was split. Solid line = North, dotted = East, dot dash = West, short dash = South, long dash = British Isles. Map produced using R package 'birdring' (Korner-Nievergelt and Robertson 2014).

8.3.2 Dispersal

The dispersal dataset included the movements of birds first captured in the summer, and recaptured in any subsequent summer. To avoid violation of assumptions of non-independence, only the furthest movement of each individual was considered if there was more than one recovery during the same summer. The mean distances of recoveries were calculated for all birds and each region independently. Similarly, we calculated the mean and standard deviation of the direction of recoveries using circular statistical methods, following Mardia (1975). Rayleigh Z tests were used to

test whether the directions of the sample came from a homogeneous distribution (Jammalamadaka and Sengupta 2001). Directions are given as cardinal directions, where 0=North, 90°=East, 180°=South, 270°=West. All circular statistics were conducted in R package 'circular' (Agostinelli and Lund 2013). Chi-squared tests were used to investigate whether the number of recoveries recorded was as equal between sex, age and regional categories.

Subsequently, to explore whether the age or sex of a bird had an effect on the distance of summer to summer recoveries, birds of unknown sex, or unknown age were removed from the dataset. The influence of age and sex on the summer to summer recovery distance was then investigated within a general linear model framework. We log transformed the distance of the recovery ensuring a normal distribution. The distance of the recovery was the response variable. Predictors were i) age, either adult or juvenile, ii) sex, male or female iii) region of first capture iv) age and sex interaction v) age and region interaction vi) sex and region interaction. The fit of the full model, which included all covariates, was assessed using chi-squared goodness of fit tests and graphically diagnosing the degree of normality in the residuals. Starting with the full model, a backwards stepwise approach based on the AIC values of each candidate model was used to find the most parsimonious model.

8.3.3 Seasonality

The seasonality dataset included all recoveries of birds first captured in the summer, and then recovered during any other month of the year. If a bird was recovered twice in the same month, only the furthest distance recovery was included in the analysis. Mean distances and directions were calculated in the same way as the dispersal analysis. Movements were modelled over the time of year of the recovery, represented as a continuous integer which counted progressively the number of the month in which the recovery occurred, with the first month being September and the final month being the subsequent August. We tested for the presence of 'out and back' movements, which may suggest a seasonal aspect to the movement patterns, using linear models fit with both linear and quadratic terms of time: support for a quadratic term suggests out and back seasonal patterns, whereas support for only a linear increase in distance with the number of months from September suggests recoveries of birds tended to be farther away as time progressed. The region in which the bird was first captured was included in the model, as was the interaction between region and the linear and quadratic terms of time since September. Model fit assessment and model selection was conducted in the same way as the dispersal analysis.

Initially, only records of known age and sex were included in the seasonality model, limiting the dataset to 1292 recoveries. The lack of influence of age or sex on these models (see results) meant these terms could be removed from the model, and consequentially that records with unknown ages and sexes could be included, increasing the dataset to 1675 recoveries.

8.3.4 Migratory Periods

This dataset captured the directionality and distance of movements of birds during the autumnal and spring migratory periods. All movements of birds first caught in summer and then recovered in any subsequent winter were considered autumnal, while movements of birds first caught in winter and recovered in any subsequent summer were spring movements. Mean distances and directions were calculated for each migratory period. In the same ways as the dispersal analysis, models were fit to investigate the influence of sex, age and region of first capture on the distance of recoveries in each migratory period. This was conducted using normal linear models with the log transformed distance of the recoveries as the response variable and sex, age, region of first capture and their interactions as explanatory variables. Subsequent models were also run that excluded the age and sex variables, allowing inclusion of records of unknown age and sex. We then investigated whether there were consistent changes in direction between autumn and spring migrations which may suggest regularity to the movements. The directions of movements between each migratory period were first visually assessed using density plots. These were produced using a Gaussian smoothing kernel with Silverman's (1986) 'rule of thumb' automatic bandwidth selection procedure. Non-parametric Watson-Wheeler tests (Agostinelli and Lund 2013) were then used to assess whether the mean distributions of bearings were homogenous between the migratory periods.

8.4 Results

8.4.1 General Recoveries

Figure 8.2 shows all the movements of Bearded Reedlings recorded in the EURING databank. The majority of the recoveries occurred in west Europe, while there were few recoveries from the south region (*Table 8.1*). 1279 recoveries occurred in the summer, while 2859 occurred in the winter. Mean recovery distance was 84.4km (median: 45km, SD: 112.72, min 6km, max 962km). *Table 8.1* details mean distance and direction in each region.

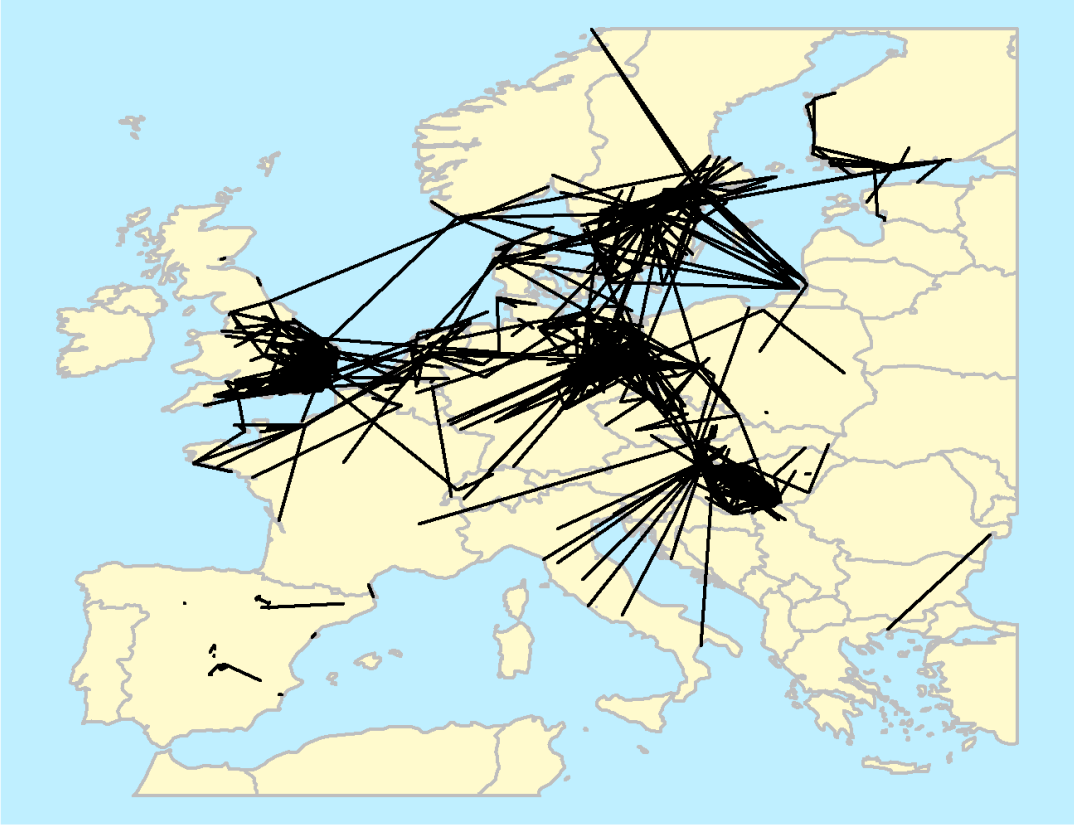

Figure 8.2 –Lines representing 4138 Bearded Reedling ringing recoveries throughout Europe recorded from1954 to 2011.

8.4.2 Dispersal

Overall, the mean summer to summer dispersal distance was 72.6km (median: 47km, SD: 71.04, min: 6km, max: 574km). For the entire dataset, surprisingly, dispersal movements were significantly directional (mean: northwest, 307°, SD: 1.95; where 0° = 360° = North; Rayleigh test: Z=0.15 P<0.001, n=398). Significant directionality held for all regions except for the north, where summer to summer recovery directions were inhomogeneous (*Table 8.1*).

After omitting records with unknown sexes and ages, 126 females (19 adults, 107 juveniles) and 185 males (38 adults, 147 juveniles) were included in the analysis of dispersal distance. The ratios of adult to juvenile recoveries were similar between sexes (proportion of adult males = 66%; juvenile males = 57%; $\chi 2_{1, 311}$ = 1.15, P=0.25), and so were the ratios of sexes within the different regions (proportion of males in north = 61%; east = 59%; west = 58%; UK = 58%; south = 67%; $\chi 2_{4, 311}$ = 1.05, P=0.90). However, proportions of adults moving in southern regions were significantly higher than the proportions of adults moving in other regions (proportion of adults in north = 28%; east = 20%; west = 7%; UK = 14%; south = 58% $\chi 2_{4, 311}$ = 42.51, P<0.001). The general linear model explained little of the variation in summer to summer recovery distances of Bearded Reedlings (R^2 = 0.03). In this full model, there was no evidence that either sex or age had an effect on the summer to summer recovery distances (males relative to females: 0.08, ± 0.30 SE, $T_{7, 303}$=0.30, P=0.77; juveniles relative to adults: 0.24, ± 0.27 SE, $T_{7, 303}$=0.90, P=0.37). From all the terms included in the full model only the region of the initial capture was retained after the model selection procedure. Based on this maximal dataset, birds from southern regions showed lower dispersal distances relative to all the other regions (region south: -0.86, ± 0.22 SE, $T_{5, 306}$=-3.91, P<0.001).

All Recoveries

Region	No. Recoveries	Mean, median, (SD) of Distance km	Mean Direction °	Rayleigh Test of Direction
North	524	137.9, 94, (147.7)		
East	613	74.4, 35, (92.7)		
West	1827	83.8, 36, (111.1)		
UK	1080	70.0, 44, (81.8)		
South	94	28.6, 20, (33.8)		

Dispersal (Summer to Summer)

North	48	102.1, 83, (96.2)	107	P=0.712
East	93	90.6, 52, (118.1)	12	P<0.001
West	147	83.6, 73, (88.3)	322	P=0.004
UK	76	72.4, 54, (60.6)	273	P=0.003
South	34	25.6, 22, (26.1)	242	P<0.001

Migration (Autumn | Spring)

Region	No. Recoveries		Mean, median, (SD) of Distance km		Mean Direction °		Watson-Wheeler Test
	Autumn	Spring	Autumn	Spring	Autumn	Spring	
North	52	21	156.1, 119, (166.2)	114.1, 70, (144.7)	181	37	P<0.001
East	197	75	68.1, 35, (83.9)	96.0, 37, (104.43)	165	340	P<0.001
West	533	161	86.2, 30, (120.6)	105.8, 76, (118.2)	239	26	P<0.001
UK	379	122	68.6, 51, (67.61)	96.1, 51, (126.0)	260	61	P<0.001
South	6	19	12.2, 10, (5.2)	34.2, 9, (63.1)	201	276	P=0.646

Table 8.1 – Summary statistics for recoveries included in the full, dispersal, and migration datasets. Trends in the directions of recoveries were considered only in datasets where they would be biologically meaningful. In the dispersal dataset, significant Rayleigh tests suggest homogeneity in the direction of recoveries. The migratory dataset is split between recoveries occurring in the autumn (summer to winter) and spring (winter to summer) migratory periods. Significant Watson-Wheeler tests, conducted in the migratory dataset, suggest recoveries occurring during the Autumn and Spring migration come from distinct distributions; direction refers to cardinal directions, where 0=North, 90°=East, *180°*=South, *270°*=West.

8.4.3 Seasonality

Recovery distances and directions of birds first captured in summer and then recaptured at any other time are detailed in *Table 8.1*. These distances were unaffected by the sex and age (males relative to females: -0.29, ± 0.18 SE, $T_{18, 1274}$=-1.57, P=0.12; juveniles relative to adults: -0.27, ± 0.16 SE, $T_{18, 1274}$=-1.68, P=0.092). Therefore, we extended the models to include records of birds with unknown age and sex. *Table 8.2* details the effects of the terms included in the most supported model after the stepwise selection procedure. Including the region of first capture in the model significantly improved the model fit in comparison to the seasonal model without a term for region (likelihood ratio test, χ^2_{12} = 148. 94*, P* < 0.001). There was significant support for a quadratic shape in the distances of recoveries over the number of months since summer in the north, UK, west and east regions, but not in the southern region (*Table 8.2, Figure 8.3*). The southern showed a significant linear shape but not support for a quadratic shape. This interaction, between the quadratic term and the region of first capture, significantly improved model fit, when compared to the additive model without the interaction (likelihood ratio test, deviance = 29.08, df=8, P=0.003).

Covariates	**Estimate**	**Standard Error**	**T-Value**	**P-Value**
Intercept	4.48	0.07	56.64	< 0.001
No. months since summer (Linear)	-5.03	3.04	-1.56	0.098
No. months since summer (Quadratic)	-5.83	3.24	-1.80	0.073
Region (north as reference level)				
East	-0.73	0.10	-7.02	<0.001
West	-0.80	0.09	-8.87	<0.001
UK	-0.71	0.10	-7.44	<0.001
South	-1.83	0.36	-5.02	<0.001
No. months since summer (linear) interaction with region (north as reference level)				
East	13.36	3.85	3.48	0.001
West	12.89	3.57	3.61	<0.001
UK	10.47	3.86	2.71	0.007
South	23.74	11.30	2.10	0.036
No. months since summer (quadratic) interaction with region (north as reference level)				
East	-2.61	4.27	-0.61	0.541
West	-0.54	3.70	-0.16	0.884
UK	-4.20	3.93	-1.07	0.285
South	19.67	9.88	1.99	0.046

Table 8.2 – Effects, standard errors, T-values and significance of covariates retained in the most supported seasonal distance linear model. N=1675, Df=15, 1660.

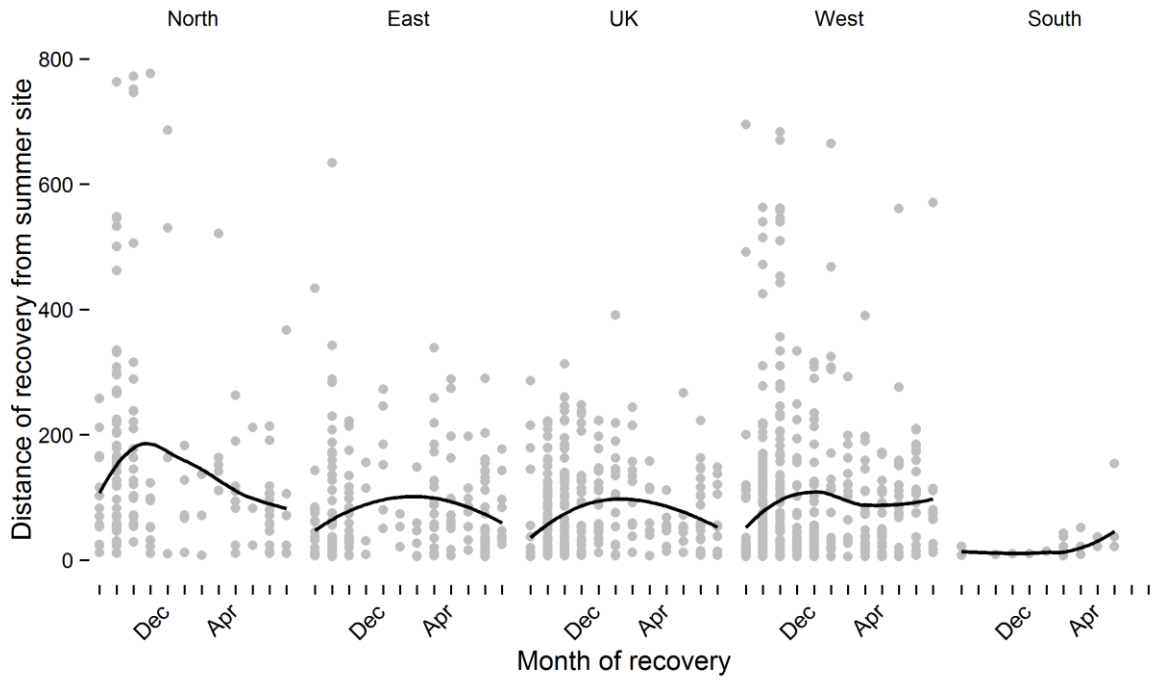

Figure 8.3 – Recovery distances of Bearded Reedlings from their summering sites in different regions of Europe over the year. Lines are Loess smooths.

8.4.4 Migratory Periods

In the autumn migratory period, represented by summer to winter recoveries, the mean recovery distance was 86.7km (median: 45km, SD: 108.23, min: 6, max: 777). In the spring migratory period, represented by winter to summer recoveries, mean distance was 100.0km (median: 53km, SD: 122.01, min: 6, max: 946). However, at all times of year some of the birds were recorded near the breeding grounds (within 10km). In the autumnal migration period, there was no influence of sex or age on the recovery distances (males relative to females: -0.03, ± 0.07 SE, T_{974}=0.41, P=0.68; juveniles relative to adults: 0.21, ± 0.12 SE, $T_{3, 974}$=-1.67, P=0.09). When individuals of unknown age and sex were included, the GLMs suggested significantly higher recovery distances from birds first captured in the north region (north: 0.93, ± 0.12 SE, $T_{5, 1272}$=7.59, P<0.001) and significantly lower recovery distances in the south (south: -1.17, ± 0.48, $T_{5, 1272}$=-2.42, P=0.015). During the spring migration, sex also had no effect on recovery distance (male relative to female: -0.05, ± 0.23 SE, $T_{3, 102}$=-0.22, *P*=0.82), but birds first captured as juveniles showed significantly lower recovery distances than adults (males relative to females: -0.87, ± 0.22 SE, $T_{3, 102}$=-3.88, *P*<0.001). When individuals of unknown age and sex were included, the southern region showed significantly lower recovery

distances (south: -1.08, ± 0.31, $T_{5, 450}$=-3.49, *P*<0.001) than all other regions during the spring migratory period.

Mean direction differed between the seasons. In the autumn, birds moved to the south, 190° (SD: 1.79, Rayleigh test: Z=0.20, P<0.001), whereas in spring mean direction was to the north, 17.3° (SD: 1.85, Rayleigh test: Z=18.1, P<0.001). Overall, Watson-Wheeler tests suggested birds moved in distinct, opposite, directions during the main migratory periods ($F_{1, 1730}$=465.94, P<0.001). This distinct directionality was preserved in birds first captured in the north, east, west and UK regions; however, birds from southern Europe showed no distinct directionality between the migratory periods (*Table 8.1, Figure 8.4*).

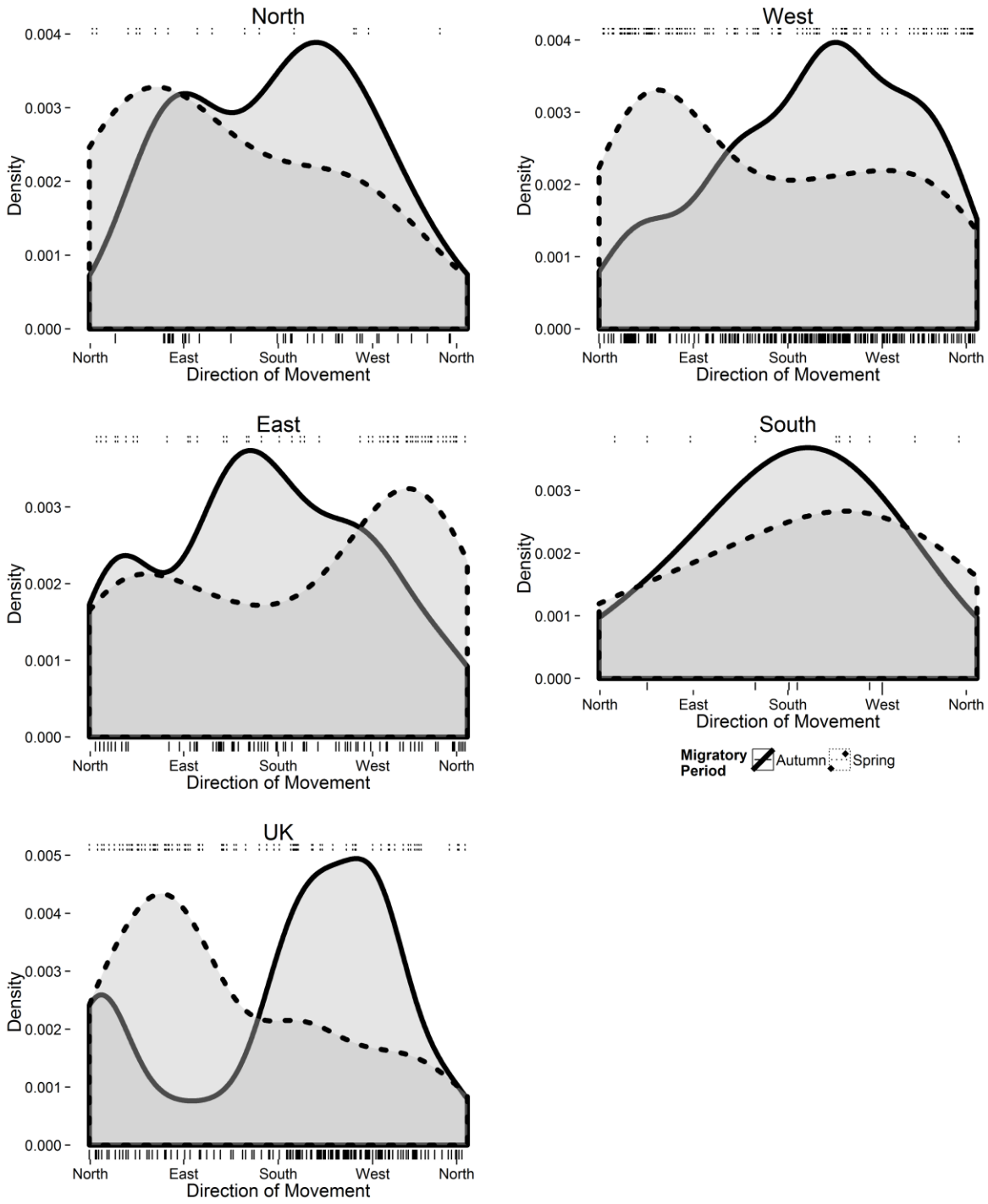

Figure 8.4 – Density plots of the recovery directions of Bearded Reedlings during the autumn and spring migratory periods. Plots shown for each of the separate regions of first capture. Rugs as above and below the curves represent sample sizes in spring and autumn respectively.

8.5 Discussion

Our analysis of European-wide ringing recoveries showed substantial movements of Bearded Reedlings both between breeding seasons, and between the breeding and non-breeding season. It also confirmed spatial heterogeneity across the five examined geographic areas. Both, dispersal and seasonal migration movements were dependent on the region in which the bird was breeding. For neither dispersal nor seasonal migration did we find any evidence of differences in recovery distances between the sexes or age groups.

Mean dispersal distances were high, and unexpectedly, for a given region, of similar magnitude as seasonal migration distances, thereby supporting the idea of links between these movement types (Elzen 1993, Paradis *et al.* 1998). The dispersal distances based on the ringing recoveries have to be interpreted with caution and are over-estimates because local recruits (within 5km) are not included. However, the high values, even compared to similar studies of other species (Helm *et al.* 2006), could be caused by the habitat specialization of Bearded Reedlings.

As this species is restricted to patchy reedbed habitat, dispersal may be critical in site colonisation and maintenance of gene flow (Greenwood and Harvey 1982, Keller and Waller 2002, Szulkin and Sheldon 2008). Similarly, Bearded Reedlings deviated from patterns reported in many other species, which show higher dispersive tendencies in a specific sex or age class (Greenwood and Harvey 1982). Our results suggested neither sex nor age had an effect on recovery distances in any region. The dependency on reedbed habitats may have shaped dispersive processes beyond traditional sex or age biased patterns. Paradis *et al.* (1998) show higher dispersal distances in wetland birds, presumably caused by the tendency for these habitats to vary in breeding quality between years. This will affect both adult and juvenile birds, potentially explaining the lack of age biased dispersal in the Bearded Reedling. Additionally, István and Csörgõ (2000) and Hofiák *et al.* (2003) show instances of 'mate fidelity' in this species, with young birds forming pair bonds which persist even during longer distance movements. Birds undertaking dispersive movements in pairs could cause similar dispersal distances between sexes, and may be adaptive for species dependent on patchy, unpredictable habitats, where dispersal may result in movements to unoccupied sites. Lastly, our analysis of dispersal also revealed unexpected directionality in all but the northern regions, and an overall tendency for northward movement. We speculate that this directionality may be associated with the northward expansion of many species, as recently elaborated for British birds (Gillings *et al.* 2015).

Seasonal movements, between summer and winter sites, were overall more regular than we had expected, although regional differences were apparent. In all examined areas, Bearded Reedlings were present near the breeding sites (i.e., within 10km) throughout the year. However, in all regions, except for the south, recoveries showed significant annual changes in distance (*Figure 8.3*) and in direction (*Figure 8.4*). Bearded Reedlings breeding in south Europe had the lowest recovery distances at every level of analysis, and did not show seasonal changes in either distance or direction. Instead, we saw a linear increase in recovery distances throughout the year, with no return movement. Peiro (2013) offers a summary of ringing recoveries of Bearded Reedlings in Spain, concluding that the major populations are sedentary with only 5% of recoveries occurring over 50km. The same study also reports some indication of higher recovery distances in male Bearded Reedlings, although effects were not statistically significant. Finally, the residency of this population was further confirmed by the lack of distinct directionality between the main migratory periods. The results support the traditional classification of this species as sedentary in this region and suggest that its longer-distance movements are likely to be dispersive.

In the remaining regions, the patterns of movement showed seasonality of distances and distinct changes in direction during the migratory periods. The recovery distances tended to be further away from the breeding sites during the winter before becoming reduced in months during the breeding season, suggesting that the birds move away from the breeding sites during the winter and return in subsequent summers. This places Bearded Reedlings, in the overall analysis, in the position of a partial migrant in much of its European range. The corresponding, more scattered, wintering distribution has also been demonstrated by Surmacki and Stepniewski (2003) for Bearded Reedlings in Poland. Limitations imposed by specific habitat requirements during the breeding season, such as reliance on large, dense reedbeds, could lift in the winter, allowing birds to exploit a more general range of non-breeding reedbeds. Hoi and Hoi (2001) suggest Bearded Reedlings show a preference for dry reedbeds at this time, as these allow seed foraging in the litter layer. Alternatively, winter movements could occur when breeding sites become unsuitable, possibly due to flooding events, frost or seed failure. Such 'weather movements' (Elkins 1988, Wernham *et al.* 2002, Balmer *et al.* 2013) are typically associated with eruptive and facultative migration. However, we consider this explanation unlikely, as recovery distances started to increase well in advance of winter in all four migratory regions (*Figure 8.3*). Migratory departure of Bearded Reedlings at a defined time of year, prior to unsuitable conditions in winter, has also been associated with a particular behaviour: Bearded Reedlings perform autumnal "high flights" in the reed beds, which initiate the subsequent departure of some birds, and which have been interpreted as display of migratory restlessness (Spitzer 1972, Pearson 1975, Elzen 1993).

Nonetheless, there were also clear differences in migratory patterns between the remaining regions. Birds first ringed in summer on the British Isles showed longitudinal movement patterns, in keeping with the climatic gradient of milder conditions in the Gulf-stream exposed western shores of the British Isles. Bearded Reedlings exploiting western sites throughout the UK during the winter months concentrated in south east England in summer. Pearson (1975) and Cramp and Perrins (1993) report similar movements of populations in England. We also provide evidence that the UK receives wintering birds which were recorded in Belgium and the Netherlands at other times, indicating that despite their small and rounded wings, Bearded Reedlings can readily move across the British channel (Figure 8.2) (see also Elzen 1993).

The west, east and northern populations showed more classical directional tendencies, which would be expected in continental migrants. Dürr *et al.* (1999) report long distance, directional, movements of Bearded Reedlings ringed in Germany towards the south west in the autumn. We show similar strong directional movements of Bearded Reedlings from west and east Europe. Finally, birds from the northern regions moved southward in autumn and north in spring, and showed the longest recovery distances. The consistency in the seasonality and directionality of movements in these populations suggests they are akin to those undertaken by short distance, but regular, partial migrants (Newton 2008, 2011).

Our findings did not support the hesitation to move that we had predicted based on the Bearded Reedlings' adaptations to endure winter in the breeding habitats. From other migratory species, the need to move is known to impose restrictions onto morphology. Nowakowski *et al.* (2014) show increasing wing length with migration distance between species of Reed and Bush Warblers. Longer, pointed wings are efficient during long distance migration, while short, rounded wings allow manoeuvrability, important for local habitat use and predator evasion (Winkler and Leisler 1992, Senar *et al.* 1994, Lockwood *et al.* 1998). The short rounded wing of the Bearded Reedling is clearly optimised towards residency, with apparently little restrictions imposed by migration (Peiro *et al.* 2006). Additionally, the seasonal changes in gut, allowing a shift in diet between summer and winter further demonstrate adaptation towards residency and away from movement. Other species show similar changes in morphology in relation to seasonally changing resources (Morton and Morton 1987, Walsberg and Thompson 1990, Greenberg *et al.* 2013), for example, resident Nuthatches, *Sitta europaea,* are known to show changing bill dimensions throughout the year (Matthysen 1989).

Our results, which demonstrate the regular mobility of a specialist resident, are important in emphasising that, despite strong adaptations to residency, highly specialist species can show

movements that resemble regular partial migration, and long dispersal distances. Our results further support the notion that exposure to severe seasonal conditions are a key factor when determining the position of a population upon the migratory continuum. Low latitude populations were sedentary, while those exposed to marked seasonal changes, where adverse conditions are more frequent, undertook more consistent movements. Climatic change is predicted to bring an increase in extreme weather events (IPCC 2007) which could have significant implications for survival if individuals were to inflexibly remain in their breeding areas. Thus, its flexible suite of movement patterns may be advantageous for the Bearded Reedling's ability to cope with climatic change and to occupy an extensive breeding distribution range.

8.6 Acknowledgements

We would like to thank the EURING databank for providing the ringing data, and especially Chris Du Feu for assistance with their use throughout. We would also like to thank Stewart White and Ian Newton for critical insight and comments and Fraenzi Korner-Nievergelt for comments on the analysis. Finally, we'd like to thank all of the bird ringers, and bird ringing schemes throughout Europe for collecting these valuable data.

Chapter Nine

General Discussion

9.1 Introduction

The Bearded Reedling has a strong affinity to its specialist habitat, *Phragmites* reedbeds. This thesis aimed to explore and progress our understanding of this relationship by exposing the population trends, habitat preferences and movement systems of this otherwise elusive passerine at the Tay Reedbeds in Scotland. It aimed to demonstrate the value in understanding space use systems when exploring questions relevant to the conservation of rare, specialist species. These questions may lie over a wide range of spatial scales, from local-scale foraging choices, to wide-scale changes in species' distributions. The restriction of the Bearded Reedling to reedbeds allowed an apparent division of these scales, and consequentially division of the thesis into local-scale, within-reedbed, space use and wide-scale, between reedbed, movements and space use. However, the research also emphasised the importance of considering a temporal, seasonal axis when acting to conserve this species, with temporal changes in space use being a common theme throughout many of the research chapters. Here, the findings of the thesis are reviewed along this temporal axis, moving from summer breeding tendencies, through autumnal behaviours and into wintering. While offering a seasonal perspective to the life-cycle of the Bearded Reedling, areas where increased conservation efforts or further research might provide distinct benefits are highlighted. The thesis concludes by detailing how this research can be translated into a proposed, effective conservation strategy.

9.2 Breeding Season

The Bearded Reedling is known to invest heavily in the breeding season, having a high reproductive output. The breeding season begins in mid-March in many previously studied populations (Spitzer 1972, Bibby 1983, Surmacki and Stępniewski 2007). Several behavioural traits allude to an urgency to begin breeding early in this species. Monogamous pair bonds are in place prior to the beginning of breeding, having often been established in the previous year for first year birds, within few months after fledging (Griggio and Hoi 2011). Additionally, the local residency of many individuals may also lift constraints to breeding onset that might be imposed by distant and regular migratory movements (Newton 2010, Leisler 2011). Further evidence of an urgency to breed is apparent in the rapid relaying times of the Bearded Reedling and the production of multiple broods over a long breeding season (Bibby 1983, Wilson 2005).

As a result of these factors, in successful years, a single pair of Bearded Reedlings may have up to four broods. This reproductive output is high relative to other resident species of woodland or farmland birds (such as Chaffinches, *Fringilla coelebs,* or Yellowhammer, *Emberiza citrinella,* Weidinger 2001). Woodland Blue Tits, *Cyanistes caeruleus,* produce one brood over the season, with a brood size of around ten young despite being similarly monogamous and unrestrained by migration. This difference is associated with differing patterns of invertebrate abundance between the habitats (Bibby 1983). Over the summer reedbeds are highly productive wetland ecosystems, with a number of invertebrate peaks occurring over the season. This is in contrast to woodland systems which may have single peak in food abundance around June, to which chick provisioning stages must be well synchronised. Even within the reedbed specialists, the productivity of the Bearded Reedling is remarkable. Both Reed Buntings, *Emberiza schoeniclus,* and Reed Warblers, *Acrocephalus scirpaceus,* will have shorter seasons, fewer broods and fewer young per brood (Leisler 2011).

A successful approach to the conservation of the Bearded Reedling may, therefore, be to exploit this high reproductive potential, providing conditions that facilitate successful breeding over an extended season, increasing abundance and consequentially, distribution. In order to achieve this, a better understanding of how both local-scale and wide-scale processes influence breeding is critical. Currently, Bearded Reedlings are considered sessile specialists that are highly dependent on the quality of their reedbed system when breeding (Bibby 1983, Campbell *et al.* 1992, Cramp and Perrins 1993). It is suggested from previous studies that the highest quality reedbeds, and those with most adequate breeding conditions, should offer heterogeneity in structure (Hawke and Jose 1996, Trnka and Prokop 2006, Trnka *et al.* 2014). This variation is thought to drive temporal and spatial diversity in invertebrate prey that is likely to offer the greatest benefits to Bearded Reedlings which are wholly insectivorous during the summer (Bibby 1981). Variation in reed structure is also known to offer a range of nesting locations that can impact on breeding success (Batáry and Báldi 2004, Báldi 2005, Vadász *et al.* 2008). Reedbed management in the form of reed cutting is a means by which heterogeneity can be achieved in a reedbed system and is, thus, often undertaken for the benefit of reed specialists (Hawke and Jose 1996, Graveland 1999, Poulin and Lefebvre 2002, Schmidt *et al.* 2005, Trnka *et al.* 2014). The research in this thesis was able to contribute to our understanding of the Bearded Reedling's breeding system and how local reedbed management might influence breeding success.

The research offered further evidence that the Bearded Reedling can be extremely prolific when breeding, even in high latitude populations such as the Tay (Chapters 3 and 6). Bearded

Reedlings on the Tay began breeding in April which is early relative to other reedbed species, but slightly later than other previously studied Bearded Reedling populations (which tend to be birds from southern England or the continent that begin breeding in March; Bibby 1981, Hoi and Hoi 2001, Surmacki *et al.* 2003). Local habitat management should therefore ensure that sufficient standing reed is available in early spring. Chapter 6 of the thesis also suggested that, despite variation in early spring weather conditions, breeding timing was nonetheless relatively consistent between years. While any flexibility in breeding onset is likely to be driven by the need to synchronise with peak food abundance (Surmacki and Stępniewski 2007), Chapter 8 suggests that migratory constraints may have some importance in higher latitude populations. Further ringing recoveries from birds on the Tay are necessary to fully establish wide movement patterns of this population and their potential restrictions on breeding timing.

The thesis also demonstrated that the nests of this species can take only a few days to construct. Laying and incubation take two to three weeks. Chicks can be in the nest for 10-12 days before fledging. With an average brood size of 5.5 (Chapter 6; Surmacki *et al.* 2003), individual pairs may have between 15 and 20 young in a single season (Bibby 1983). Thus, encouraging a highly productive breeding season, could have important consequences for conservation on a national scale. Indeed, despite a cold start to the breeding season in 2014, the Bearded Reedlings on the Tay experienced a warm summer, resulting in the highest numbers of birds ringed on the Tay to date (Chapter 3). The population in 2014 was around 30% of the total number of birds on the British Isles. This year also saw the first recoveries of Tay birds outside of the Tay area, with birds occurring in reedbeds up to 50km away, suggesting high numbers may encourage an expansion in distribution. Thus, methods by which to facilitate productivity during the breeding season may directly influence both local and wide-scale conservation efforts.

Local-scale conservation management could offer a means to facilitate productivity, by providing optimal breeding habitat. During the breeding season, factors that may limit productivity are the availability of nesting sites, foraging resources and the influences of predation. The thesis aimed to gain insight into these factors by studying patterns in the space use of Bearded Reedlings. The clearest and most consistent spatial patterns were in the positioning of the nest itself. Bearded Reedling nests were invariably within old patches of thick, unmanaged reed (Chapters 4 and 6; Hoi and Hoi 2001). As natural Bearded Reedling nests can be difficult to locate and information from UK populations has been scarce, Chapter 6 explored the structure of a sample of nests located on the Tay. Nests are open cups and constructed using *Phragmites* stems, leaves and panicles and are positioned low, at the foot of tall reeds in areas where sufficient leaf litter has built up (Wawrzyniak

and Sohns 1986, Elzen 1993). The consistent spatial positioning of nests within these areas suggests there are important benefits associated with nesting in old reed patches. Areas with thick leaf litters are generally within the driest sections of the reedbed and may therefore be preferred if risk from inundation is minimised (Wilson 2005). These areas may also offer favourable microclimatic conditions, providing areas sheltered from precipitation or buffered against external changes in temperature (Báldi 1999).

Perhaps the most likely reason for the consistent positioning of nests within old, dense areas of reed (Chapter 6) is the minimisation of predation (Chapter 5). A diverse nest predator guild may exploit reedbeds, with Snakes, Foxes, Otters, Rats, Corvids, Gulls, Water Rail and Marsh Harriers having been reported in various predation studies throughout Europe (Graveland 1997, Albrecht 2004, Batáry *et al.* 2004, Trnka *et al.* 2014). On the Tay the highest threats to nest productivity look to come from Foxes, Water Rail and Marsh Harrier (Chapter 5). The positioning of nests within the densest areas of reed is likely to reduce the chance that nests are located by predators, with such areas often being impenetrable to larger mammalian species. The proximity of the nest to an edge may also have an important influence on nest predation rates with nests closest to the boundaries between habitats tending to have increased predation rates (Chapter 5, Batáry and Báldi 2004, Batáry *et al.* 2004). All nests on the Tay were located towards the outer edge of the reedbed, closer to the estuary than the land bank. These areas are unlikely to be readily accessible to many terrestrial species, and again suggest predation pressures are an important driver of spatial nesting patterns in this species. The research chapters demonstrate the value in understanding spatial patterns in nest positioning and associated productivity, and can be directly translated into local management strategies (see management section).

Information concerning foraging decisions during the breeding season may also benefit conservation. The provisioning of effective foraging locations could offer local management strategies a means to directly assist the productivity of the population. Chapter 4 offers the first investigation into fine-scale, individual level, habitat selection in Bearded Reedlings through use of contemporary spatial data gathering methods. While there was no overwhelming support for changes in abundance between managed and unmanaged areas of reed, when they were available, cut and young patches of reed were selected during foraging trips. The results, in line with those of Trnka *et al.* (2014), also suggested no changes in invertebrate abundance between cut, young or old reed in mosaic cut reedbeds. Thus, the selection of early successional, young areas of reed for foraging is perhaps the result of changes in the structure of reed, with more open areas offering more successful foraging (Chapter 4; Beemster *et al.* 2010). Despite this, Bearded Reedlings look to

be opportunistic, with long and directed foraging trips to ephemeral resources. Continued research, especially that which can satisfactorily map the extremely fine-scale variation throughout reedbeds, and explicitly link this variation to bird distributions or foraging trips, would be of high value when quantifying selection in these habitats. Such studies may benefit from high resolution satellite technology (Poulin *et al.* 2010, Bresciani *et al.* 2011, Zlinszky *et al.* 2012, Stratoulias *et al.* 2015), or drones (Chabot *et al.* 2014), which were unavailable during this study.

A shared theme throughout the chapters concerning the breeding season of the Bearded Reedling was that of a within-breeding season temporal axis. This is driven by the early onset and long breeding season of this species, which occurs in parallel to dramatic temporal changes in the structure of the reed (Chapter 5). As Bearded Reedlings are the only reed specialist Passerine to begin breeding prior to new growth, temporal dynamics are emphasised within this system. The research in this thesis only touches upon the potential temporal changes in breeding ecology that might occur over the season. The predation rates of artificial nests positioned on the edges of cut areas reduced considerably as new growth increased from April to June (Chapter 5). However, other factors, with potential relevance for the conservation of this species remain unexplored. As real nests were only located during April and May, temporal changes in their spatial positioning and structure that might be driven by reduced threats from predators, or changes in microclimate need further investigation. Similarly, temporal changes in resource selection during foraging trips could have significant implications for management. Such changes are likely as invertebrate food sources hatch differentially across the season. While studies of space use alone can offer important insight into ecological patterns, these patterns may be highly dynamic when considered over time, and repetition of space use studies on an appropriate temporal scale may offer a critical alternative perspective.

Overall, the research in this thesis has offered insight into the breeding biology of this elusive reedbed Passerine. Conservation efforts should aim to harness the highly productive nature of this species during the breeding season. This may be achievable through local-scale habitat management which ensures appropriate foraging and nesting locations are available, building on the insights in this thesis. Despite efforts on the local-scale to improve breeding conditions, the fate of many bird populations will be influenced by global climatic change. For the Bearded Reedling, consequences of climatic change are difficult to predict due to the size of this species' range and the wide geographic variation in predicted climate change. However, warmer springs may facilitate earlier breeding, and a productive season (Surmacki and Stępniewski 2007). Additionally, the tendency for reedbeds to be consistently high in invertebrate abundance throughout the season,

rather than during short temporal peaks, should reduce the chance of this species becoming unsynchronised with food resources. To complement the strong foundation on which to base local-scale habitat management, further research into potential consequences of climate change for this species is necessary.

9.3 Autumn

Previous research (Axell 1966, Spitzer 1972, Pearson 1975, Peiro *et al.* 2006, Peiro 2013), combined with the local and wide-scale findings of this thesis (Chapters 3, 4 and 8), suggest that Bearded Reedlings are faced with a critical choice in autumn: to remain locally resident within their breeding reedbed, or to move at a wider-scale, between reedbeds. In late September through October 'high flying' activity is almost a physical representation of individuals making this decision. This behaviour involves groups of individuals flying rapidly above the reedbeds in varying directions, before landing considerable distances from their origin. The majority of these flights result in birds landing elsewhere in the reedbed (Spitzer 1972, Pearson 1975). However, Spitzer (1972) suggests that in high population densities, high flying activity becomes increasingly excited, eventually resulting in small groups leaving the local reedbed. Thus, the decision to remain local or leave could be mediated by local population density (Spitzer 1972). As birds that remain local begin to occupy their wintering behaviours, they are discussed in the subsequent 'winter' section, with the current section focusing on the moving proportion of the population.

As Bearded Reedlings have such a strong affinity with reedbed habitats, and a large proportion of the population remains within a single reedbed for the entire year, wider-scale movements were traditionally considered rare in this species. There are only a few previous studies that allude to the occurrence of more frequent wider-scale movements (Axell 1966, Spitzer 1972, Pearson 1975, Dürr *et al.* 1999). These wider-scale movements may be the result of dispersal, weather driven eruptions or more consistent, migratory patterns. The research in this thesis aimed to clarify the patterns in wide-scale movements of Bearded Reedlings. The wide-scale ringing analysis presented in Chapter 8, redefines the traditional categorisation of the Bearded Reedling as a largely sessile resident. Instead, long distance movements of between five and 100km look to be relatively frequent and, in some areas, temporally consistent between years. Dispersal looks to be the major incentive for movement in areas that experience mild winters, such as populations in reedbeds in Spain or Italy. In more northerly regions birds look to move at consistent times of year with clear directional gradients which resemble migration.

Dispersive movements in Bearded Reedlings are likely to be critical for adequate gene flow, with sessile and isolated populations likely to be at risk from inbreeding (Marin and Marchesini 1994). Further, the formation of pair bonds in the post-breeding season, during post-juvenile moult, and thus prior to any local dispersive movements, could theoretically result in pair bonds between siblings. Despite this, using DNA fingerprinting, Marin and Marchesini (1994) fail to reveal inbreeding in a small population of Bearded Reedlings in Italy and suggest unseen immigration must be facilitating gene flow. The results from the wide-scale ringing analysis confirm more frequent wider movements than expected in this species, which should mitigate risks from inbreeding. In Chapter 8, distances moved by Bearded Reedlings between summers were similar to those expected from waterbirds dependent on isolated and ephemeral wetland resources (Paradis *et al.* 1998). There was also little evidence of increased dispersal distances in either sex or age group, suggesting sex-biased dispersal is not the main mechanism by which inbreeding is avoided in this species. Other processes such as kin recognition during early pair bonding, the production of single sex broods, and extra-pair mating may also have a role in maintaining a healthy genetic environment (Hoi 1997, Hoi and Hoi-Leitner 1997, Keller and Waller 2002) and should receive further investigation.

Interestingly, the ringing analysis also suggested that summer to summer dispersal distances over the last 40 years had the tendency to be in a northward direction. While preliminary, such patterns may have important implications for wide-scale conservation. An increasing northward dispersal tendency may suggest gradual climatic change is permitting an expansion in this species' range. More northerly areas may begin to offer productive breeding sites, or increasingly mild, tolerable wintering conditions. The Tay Reedbeds demonstrate the importance, both for local abundance and wide-scale distribution that colonisation events can entail. Extensive ringing and monitoring conducted on the reeds suggests, with some confidence, that Bearded Reedlings first occupied the Tay in 1992 when the first individuals were captured in mist nets. This population now forms a significant proportion of the UK population (Chapter 3), and has relevance at an international scale, being towards the current northern limit of the species' range. Indeed, recent highly productive years have led to sightings and recoveries of Tay birds in more northerly reedbeds. The potential for continued northward expansion of this species should be monitored, and, providing extensive areas of suitable habitat are available, could have marked influence over its conservation status.

The results in this thesis also suggest that northward expansion is feasible in that, through a relatively flexible movement system, Bearded Reedlings can cope with an array of seasonal conditions. Chapter 8 argues that consistent, north-south migratory movements can occur in the

most northerly parts of this species' range where there are predictable changes in climatic conditions between seasons. Similarly, in more intermediate regions, birds show a looser winter distribution, occupying non-breeding reedbeds that tend to be drier (Axell 1966, Surmacki and Stepniewski 2003, Surmacki and Stępniewski 2007). Further research, possibly using a combination of telemetry and capture-recapture methods, is required to establish any geographic changes in the proportion of the population that remains resident. Such research is critical in establishing the importance of any genetic predisposition to movement, and whether movements are anticipatory. Additionally, the potential role of density dependence as a mediator of movements needs further investigation (Spitzer 1972). In a system where high productivity can result in high numbers of individuals in limited geographic areas, and where resources are restricted to a single reedbed, density dependent winter dispersal would be an intuitive means to avoid high levels of intraspecifc competition. Studies of this system could therefore offer important conclusions for our wider understanding of animal movement systems and how these relate to overall population dynamics.

9.4 Winter

The strict specialisation of the Bearded Reedling to reedbed habitats is most apparent during the wintering period. While species such as the Reed Warbler migrate, and others such as the Reed Bunting begin to exploit more general habitats, Bearded Reedlings remain rigidly dependent on reed stands during the winter. This is permitted by a distinct change in diet that occurs in October, from summer invertebrate prey to a winter diet of reed seed. Internally, this involves a considerable change in gut morphology, where the gizzard becomes lined with keratinous plates, doubling in size and increasing the total body weight by up to 5% (Spitzer 1972). Throughout the winter, though most intensively during September and October, birds begin to ingest grit (Wilson 2014) which they hold within their gizzard to assist the breakdown of reed seed. The timing of these wintering preparations for birds that undertake wider movements during the early autumn are unclear, with the increased weight and lower nutritional value of reed seed likely to make movement inefficient.

During the winter, food abundance and access to food, as well as direct impacts from local weather conditions will be key factors in survival. Wilson and Peach (2006) demonstrate this in a population of Bearded Reedlings in northern England, where the leaf litter was blocked due to winter flooding and led to high levels of mortality. It is therefore critical, when looking to conserve this species, that this key seasonal period is considered during local conservation management. The research in this thesis looked to better establish how the clear changes in ecology of this species between the summer and winter impact on local space use, and to use this information to further inform conservation strategies.

Chapter 4 suggested that, during the winter, birds look to occupy dry areas of old reed, with deep leaf litters. Almost all of the radio-tracked individuals that remained local during the September – October tracking period eventually converged into a single stretch of old, unmanaged reed. This area, and other patches of similar structure, saw highest encounter rates during point transect surveys conducted in the winter. While this old, tall reed has the longest seed panicles, individuals spend most of the time foraging among the leaf litter at this time of year. Only when the litter is flooded or frozen did birds tend to take the seeds directly from the panicles. This preference for foraging low in the reed is possibly driven by the need to reduce exposure to avian predators. Future studies should consider methodologies that allow the measurement of seeds directly within the litter layer, rather than estimates from panicle length. These may provide insight into the apparent between-site differences in winter distribution highlighted by the lack of congruence between this thesis (Chapter 4) and previous research (Beemster *et al.* 2010). For example, Beemster et al (2010) show contrasting results, suggesting that high numbers of Bearded Reedlings occupied previously grazed reed during the winter, rather than old reed patches. A number of factors, including local food abundance, food availability during various weather conditions or tidal phases, and social behaviours could influence resource selection during the winter and need further investigation.

While not explicitly investigated in this thesis, the extreme reproductive output of the Bearded Reedling highlighted in the breeding season section, could be related to the dependence of this species on reed seeds during the winter (Wilson and Peach 2006). This strict dependence is likely to result in high winter mortality in years when seed is limited or inaccessible (Wilson and Peach 2006). The high investment and productivity of the Bearded Reedling during the breeding may compensate high mortality during the winter. These traits are typical of high investment, low survival (classical r-selected, Pianka 1970) species, which tend to occupy specialist niches. Bearded Reedling populations from distinct geographic regions may offer an interesting system in which to study variation in life history strategies if less urgent breeding strategies are employed in regions with milder winters. Such research could be useful when predicting the consequences of climate change for the Bearded Reedling. While mild spring conditions may increase productivity during the breeding season, predicted increases in storm events and winter flooding could increase winter mortality.

The research in this thesis offers some of the first quantifications of space use in this species during the wintering period. This information has revealed the importance of conserving areas of old, unmanaged reed as a winter foraging resource. However, Chapter 4 suggests important

between-site variation in winter foraging resources, and further research is required to establish the factors driving this variation. Additionally, the research suggests that the high reproductive output, coupled with a low winter survival is likely to contribute to the large population fluctuations apparent in this species. These fluctuations should be considered in any monitoring strategies and when establishing population trends.

9.5 A Proposed Scenario for Conservation Management

Studying the space use of the Bearded Reedling has revealed patterns that can inform conservation strategies both at a local and a wide-scale. These patterns should be considered over a yearly temporal axis and the most effective management should offer directed conservation measures during key seasonal phases. It is critical that reed management regimes are well defined in terms of objective prior to management. Here, an ideal management strategy for the Bearded Reedling is recommended. While this advice is focused around reedbed management that improves habitat quality for the Bearded Reedling, it is likely that this prescription will generate healthy reed systems that will also benefit other features of conservation interest. Only where management motives are to reduce reed vigour, potentially to limit reed encroachment into other habitats, or maximise botanical diversity, will discrepancies exist (Hawke and Jose 1996).

The initial colonisation of the Bearded Reedling into a local system may be unpredictable due to the large temporal fluctuations in population size that this species experiences. A larger reed stand may be easier for birds to locate, and hold a wider range of reed structures and resources possibly encouraging occupation. However, birds have been known to occupy, and breed in, small fringes of reed (Bibby and Lunn 1982, Surmacki 2003). Colonisation may be more likely if the new reedbed is positioned close to current breeding populations. As eruptive and dispersive movements occur in the post breeding season, birds will tend to be most mobile during September and October (Chapter 7).

A dynamic reed management regime that aims to create heterogeneity in the structure of reed is likely to offer high quality habitat for this species (Chapters 4, 5, 6 and 7). This can be achieved by preserving unmanaged, old reed over the majority of the stand, while stimulating vigorous growth in other, more limited areas. As old, unmanaged areas may begin to naturally succeed (Hawke and Jose, 1996), management should be rotational and dynamic, with long term planning necessary to achieve the most effective strategy. Three main management techniques may be used to achieve a dynamic system: hydrology, grazing and reed cutting (Hawke and Jose, 1996). Complete hydrological control can be difficult to achieve, with stands needing to be split into

separate hydrological units. Grazing can offer immediate benefits to reed vigour, but continued trampling of reed 'runners' can reduce productivity in the long term. Reed cutting can be expensive, but offers controlled and flexible management. As reed cutting was the main focus of the thesis, is achievable, and offers both temporal and spatial flexibility, here, only this method is considered further.

Cutting regimes should aim to leave a high proportion of the reedbed as old, dry patches of reed with a deep leaf litter (Chapter 4). This will provide suitable nesting sites and winter foraging for Bearded Reedlings (Chapters 4 and 6). Adequate leaf litter depths should be around 20cm, and will need several years of layered, un-removed growth to accumulate (Chapter 6). Cutting of identified areas can then be conducted using brushcutters at the smallest sites, walk-behind mowers in intermediate areas, and may require specialist machinery in the largest stands. Patches should be cut in a mosaic and aim to maximise the variation in age structure throughout the stand (*Figure 9.1*). Cut patches offer important foraging resources for Bearded Reedlings during the breeding season and reinvigorate reed, hindering succession (Chapter 4). While single wale, yearly cutting of the same patches, produces high quality reed for thatch, rotational cutting, where cut patches are able to mature for several growing season offer highest benefit to wildlife. Rotational cutting allows colonisation by invertebrates, increases structural diversity and minimises accessibility of the stand to predators in the early season (Chapters 4 and 5). A boundary of uncut reed should be preserved between cut patches and the edges of the reedbed to further limit access to terrestrial predators.

In terms of scale, the area of the reedbed that should receive management in the form of mosaic cutting will vary based on the size of the reedbed. Areas cut in a mosaic pattern should never exceed 30% of reedbed to ensure there is adequate old reed available. However, this could be rotated around the reeded area over the long-term (*Figure 9.1).* To maximise the structural diversity in the mosaic the cut patches should be small, not exceeding more than 0.3 hectares.

The extensive areas of old, unmanaged reed should be monitored for scrub incursion through use of fixed point photography or drone mapping every three to five years. These areas are likely to be prone to succession, with the build up of the seed bank allowing pioneer species such as Common Nettle, *Urtica dioica*, and Bittersweet, *Solanum dulcamara*, to gain a foothold before wet scrub Willow, *Salex,* species and Alder, *Alnus,* begin to colonise. When these later successional stages limit reed growth, and productivity is reduced, management should be initiated in these areas, while previously cut patches are left to regenerate and mature. *Figure 9.1* suggests a long term, dynamic cutting regime.

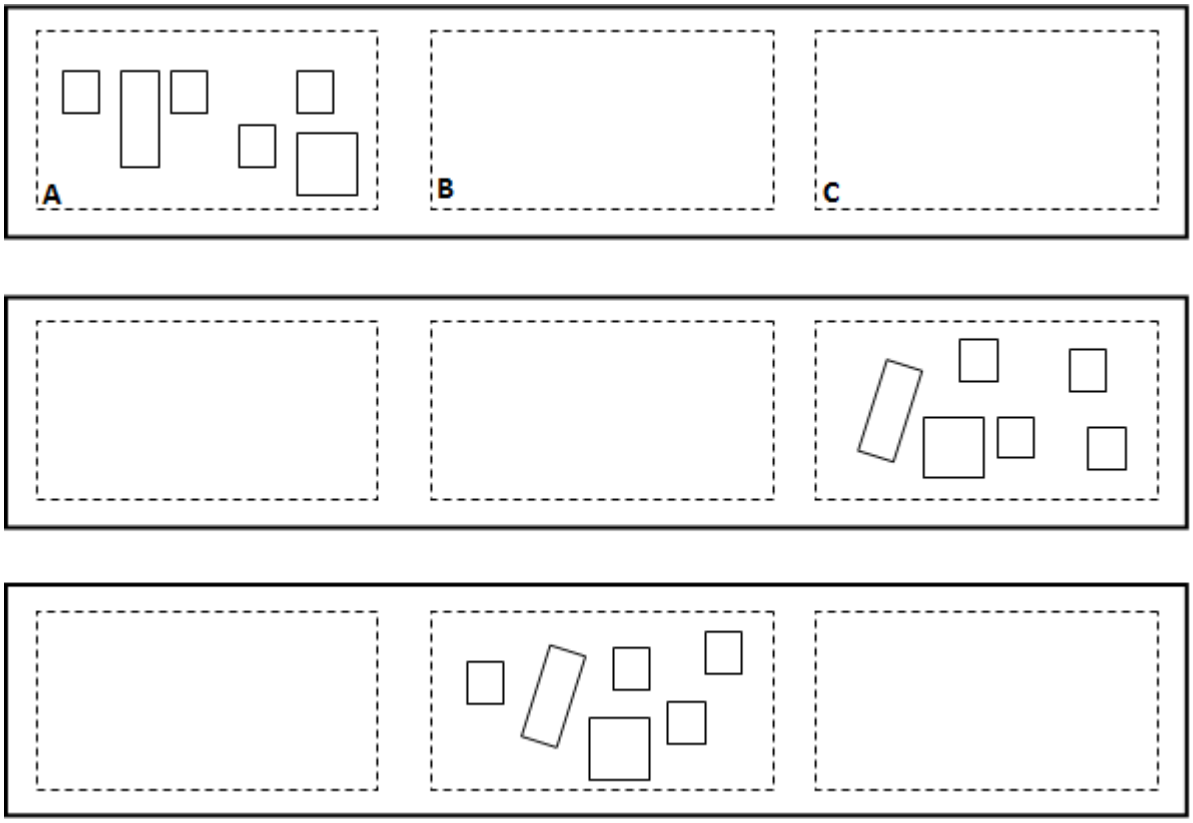

Figure 9.1 – Suggested long-term dynamic reed cutting regime. The thick solid boundary on each panel represents the extent of the reedbed. The reedbed is split into three compartments, depicted by the dashed lines. The topmost panel shows current management, where compartment A is cut in a mosaic pattern. In this compartment the small squares represent cut patches that may be cut in a given winter then left for 1-3 years before being cut again. Note compartments B and C remain uncut, offering extensive old, unmanaged reed for nesting and winter foraging. After several years reed productivity will become reduced in the unmanaged compartments. At this point, the management regime can move to compartment C for several years, reinvigorating the reed in this section. Finally, management can move to compartment B, similarly invigorating the reed while compartments A and B mature. The process can be continued indefinitely. The cutting regions which are rotated over could be any size, but the cut patches should not exceed 0.3 hectares.

In addition to an effective reed cutting regime, local-scale management should consider other means to enhance the habitat for Bearded Reedlings. The provision of supplementary food is a commonly used method to reduce mortality of other bird species during the winter. This is likely to be ineffective with Bearded Reedlings, due to their specialisation to reed seed at this time of the year, which is often locally abundant. However, the provision of grit, which is taken into the gizzard to assist the breakdown of seeds, looks to be an important winter management tool (Wilson 2014). Natural gritting areas are often limited due to inundation or snow cover. Direct provisioning of grit within trays or on bird tables within the reeds may offer a useful resource for the birds, while facilitating observations during monitoring surveys (Wilson 2014). Grit provisioning should commence in early September, and be available until February. Similarly, nest boxes specifically constructed for use by Bearded Reedlings have seen success in some sites (Wilson 2005). These have been most effective in wet reed stands, where sufficient leaf litter is unavailable to provide natural nesting areas. Artificial nests should be positioned prior to March, offering an elevated nesting position above areas of water.

After establishing a population of Bearded Reedlings, an effective monitoring protocol should be initiated. This species is difficult to monitor, with methodologies often being site specific (Chapter 7). Point counts conducted from elevated positions throughout the reedbed provide useful relative comparisons over time or between management prescriptions (Chapter 4). These should be conducted during the breeding season, with two visits during April and a third in May to capture adult activity (Chapter 4). Further counts could be conducted in the later season (May-July) when fledged young are moving freely to offer an index of productivity. However, further refinement of methods with which to monitor productivity efficiently is necessary, with the tendency of young to form large groups, increasing variance during surveys. Direct observations of nests will offer the highest quality information on productivity, but nest finding will require significant effort (Chapter 5). Walked transect surveys that require navigation of the stand are unlikely to be effective and could damage the reed.

Mist netting and bird ringing protocols can offer reasonable estimates of the population size (Chapter 3), and allow modelling of survival. As these methods require a higher effort than point count surveys, they may be most feasible when conducted intermittently. During September and October, observations should be made in neighbouring reedbeds, possibly through use of citizen science schemes, to establish whether movement is occurring, and locate new sites with the potential for management.

9.6 Conclusion

With a changing climate, and ever more limited space for biodiversity, the major motive of this thesis was to provide evidence-based advice to act as a foundation for the conservation of a rare species. As specialist species are some of the most threatened by wide-scale climatic change and local-scale habitat modification, the conservation of a highly specialist passerine, the Bearded Reedling, was at the heart of this research. Being limited to reedbed habitats, little was known about the movement systems of this species, with research into spatial patterns, distribution and movement offering invaluable insight for conservation. At a local-scale, understanding spatial patterns helped reveal abundance, nesting preferences, predation processes and foraging habits. At a wide-scale, the research demonstrated behavioural flexibility in the face of a changing climate and the critical need for across site collaboration. Together, these factors suggest the future of the Bearded Reedling looks positive. On a European scale, this species is considered 'of least concern' due to its extensive range. However, when beginning this research, within the UK the Bearded Reedling was listed as an "Amber" bird of conservation concern (Eaton *et al.* 2009). After reassessment, in December 2015, the Bearded Reedling was moved from Amber to Green status (Eaton *et al.* 2015), in light of continued northward expansions, effective local management and positive population trends to which the Tay Reedbeds have contributed considerably. This research demonstrates how studies of space use can be used to form a firm scientific foundation, and contribute to the successful conservation of rare and specialist species. With an understanding of the interactions between specialist species and their associated habitats, we can act to reduce their chances of extinction and help to mitigate the loss of biodiversity as a whole.

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